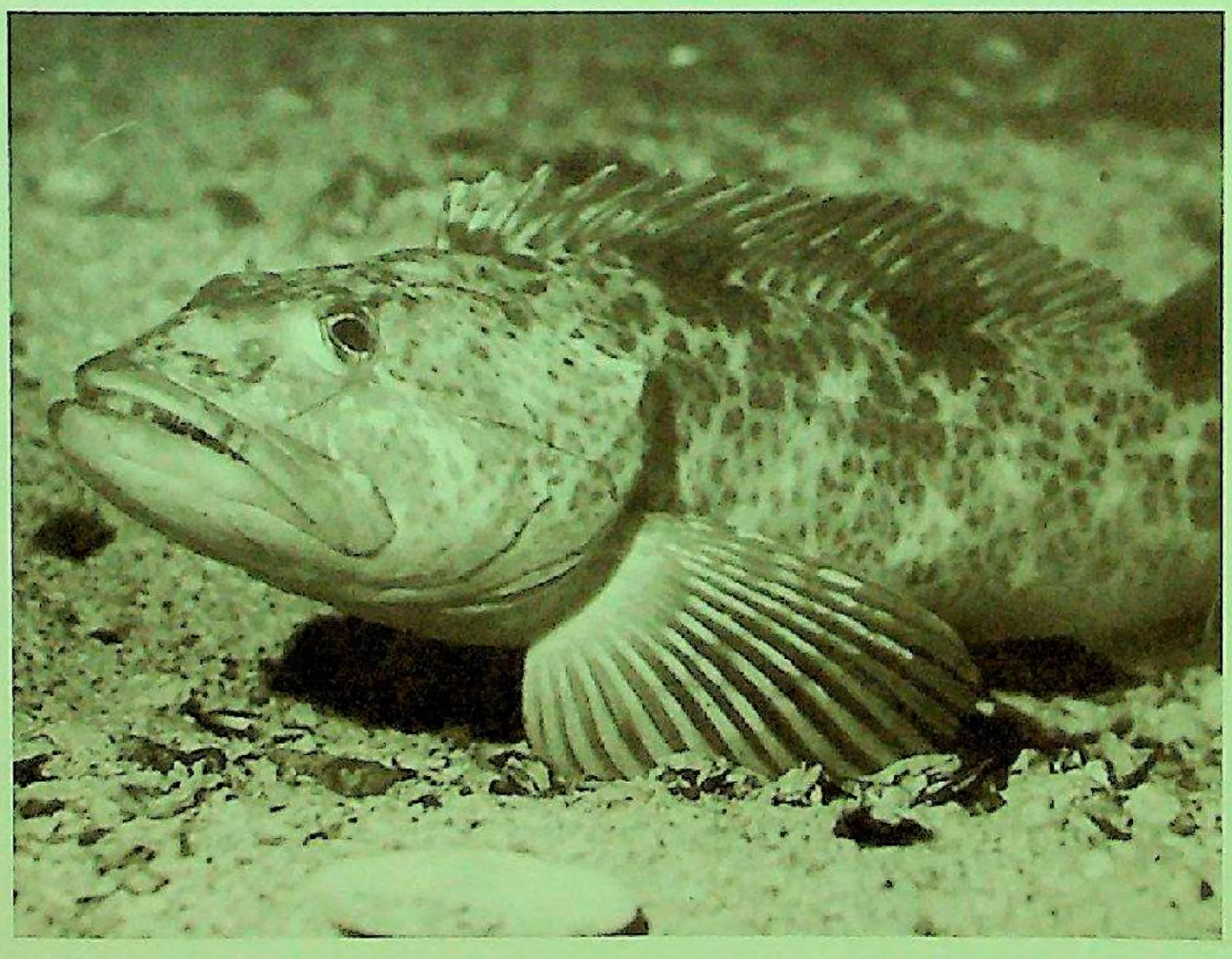
CALIFORNIA FISH and GAME

"CONSERVATION THROUGH EDUCATION"

VOLUME 83 SUMMER 1997 NUMBER 3



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VOLUME 83 SUMMER 1997 NUMBER 3

Published Quarterly by

STATE OF CALIFORNIA
THE RESOURCES AGENCY
DEPARTMENT OF FISH AND GAME
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Lingcod, *Ophiodon elongatus*
Photograph by James R. Chess, National Marine Fisheries Service, Tiburon Laboratory

ANNOUNCEMENT

The **3rd International Symposium on Aquatic Animal Health** will be held in Baltimore, Maryland, USA from 30 August to 3 September 1998. The meeting will be the first major international forum to focus comprehensive attention on a diversity of aquatic animals, including fish, shellfish, marine mammals, and sea turtles, from a diversity of habitats including aquaria, aquaculture, and the wild. The symposium venue is the Renaissance Harborplace Hotel, located in Baltimore's Inner Harbor.

The scientific program will include nine invited plenary lectures, 165 contributed oral presentations, and 200 poster presentations. Scientific sessions will include the following topics: aquarium medicine, bacteriology, carcinogenesis, emerging diseases, husbandry, immunology, legislation, nutrition, parasitology, prophylaxis, toxicology, treatments, virology, and zoonoses. Participants will have the opportunity to tour the Aquatic Pathobiology Center at the University of Maryland, the Center for Marine Biotechnology, and the National Aquarium in Baltimore. Multi-headed microscopes will be available to enable participants to review preserved material and histopathology slides. An exhibition of newly published books is planned. Abstract submission deadline is 15 March 1998.

The meeting is supported by six professional aquatic animal health organizations: American Fisheries Society - Fish Health Section (who will hold their 1998 annual meeting as an integral part of the symposium), Asian Fisheries Society, European Association of Fish Pathologists, International Association for Aquatic Animal Medicine, Japanese Society of Fish Pathology, and National Shellfisheries Association.

For additional information, visit the symposium website at: www.som1.ab.umd.edu/AquaticPath/isaahweb, or contact Dr. Sarah Poynton or Ms. Sylvia Lee, Division of Comparative Medicine, Johns Hopkins University School of Medicine, 459 Ross, 720 Rutland Avenue, Baltimore, Maryland 21205, USA; telephone: USA 410 955 3273; FAX: USA 410 502 5068; e-mail: wellfish@welchlink.welch.jhu.edu.

California Fish and Game 83(3):89-104 1997

WATER CHEMISTRY AND COMMUNITY STRUCTURE OF SALINE AND HYPERSALINE SALT EVAPORATION PONDS IN SAN FRANCISCO BAY, CALIFORNIA

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We measured water quality and community structure in a series of low (<35 ppt) to high (35-90 ppt) salinity salt evaporation ponds in South San Francisco Bay. Dissolved oxygen concentrations and pH levels were negatively correlated with salinity and showed greater variability in low salinity ponds than in high salinity ponds. Animal and plant diversity declined with increasing salinity, leading to simple but relatively stable assemblages at high salinities. Although diversity was high in low salinity ponds, assemblages were seasonally unstable. Possible causes of these temporal fluctuations in invertebrate and fish assemblages were shifts in algal production, poor water quality, and seasonal variability in immigration of organisms from the bay. Salt ponds appear to favor small fish that are tolerant of high salinity and variable water quality and prey resources. We collected 15 fish species, including six that may reproduce to 75 ppt. The remaining species were transients whose distributions within the ponds may have been limited by high salinities, poor water quality, and changing habitat requirements with age. Seasonal and annual variability in water chemistry and biological diversity of low salinity ponds appeared to be associated with the timing and duration of water inflow from San Francisco Bay. Conditions created by the closure of the ponds to tidal flow may have contributed to diebacks in macrophytes and poor water quality. Further, seasonal closure of these ponds to tidal flow prevents movement of fishes between the ponds and the bay.

INTRODUCTION

The shoreline of South San Francisco Bay (South Bay) is a mosaic of altered habitats dominated by thousands of hectares of large, shallow impoundments used in solar salt production. These salt ponds, which range in salinity from 20 to >300 ppt, provide many different and important habitats for a variety of wetland species,

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including migratory waterfowl and shorebirds (Stenzel and Page[2] 1988, Takekawa et al.[3] 1988) and other bird species more often associated with hypersaline lakes (Anderson 1970).

Previous biological studies of salt ponds have focused almost exclusively on the biology of waterbirds (Anderson 1970, Gill 1977, Swarth et al.[4] 1982) or brine shrimp, *Artemia salina*, in hypersaline ponds (Baker[5] 1966, Swarth et al.[4] 1982). The biology of pond fishes, and low-salinity ponds in general, has been neglected with the exception of studies by Carpelan (1955, 1957), who found fishes in ponds to 80 ppt. Above 80 ppt, brine shrimp and phytoplankton were the dominant members of pond communities.

The primary purpose of this study was to describe the structure of biological communities in six low to moderately hypersaline (>35-90 ppt) salt ponds in South Bay. We also examined spatial and temporal patterns of distribution in fish, invertebrate, and algal assemblages as related to variations in pond physiochemistry. Finally, we examined patterns of growth, spawning, and diet of common fish species to identify life history attributes of pond residents.

STUDY AREA

The six ponds included in this study were similar in size (100-150 ha) and depth (1-2 m) to other salt ponds of South Bay (Fig. 1). Water entered the study ponds from the bay between late spring and fall, flowing first into Pond A9, then passively or by pump into the five succeeding study ponds (A10, A11, A12, A13, and A15). Another source of water to the study area originated from Pond A8, which served as an intermittent source of high salinity water (> 50 ppt) to Pond A11. During summer and fall, water moved continuously between ponds, but in winter and early spring there were long periods when no water flowed between the ponds or from the bay.

METHODS

We monitored water movement through pond culverts and measured surface salinity with a refractometer, dissolved oxygen with a dissolved oxygen meter, pH with a pH meter, and water and air temperatures biweekly in each pond from April

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[2] Stenzel, L.E. and G.W. Page. 1988. Results of the 16-18 April 1988 shorebird census of San Francisco and San Pablo bays. Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California, USA.

[3] Takekawa, J.Y., D.S. Gilmer, C.M. Marn, H.M. Ohlendorf, L.A. Accurso, and J.E. Takekawa. 1988. Abundance, distribution and habitat use of wintering waterfowl in the San Francisco Bay ecosystem, 1987-1988. U.S. Fish and Wildlife Service, Dixon, California, USA.

[4] Swarth, C.W., C. Akagi, and P. Metropoulus. 1982. The distribution patterns and ecology of waterbirds using Coyote Hills salt ponds. U.S. Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge, Newark, California, USA.

[5] Baker, M.S. 1966. Autecology of *Artemia*: Factors influencing hemoglobin synthesis and cyst production. M.A. Thesis, San Francisco State College, San Francisco, California, USA.

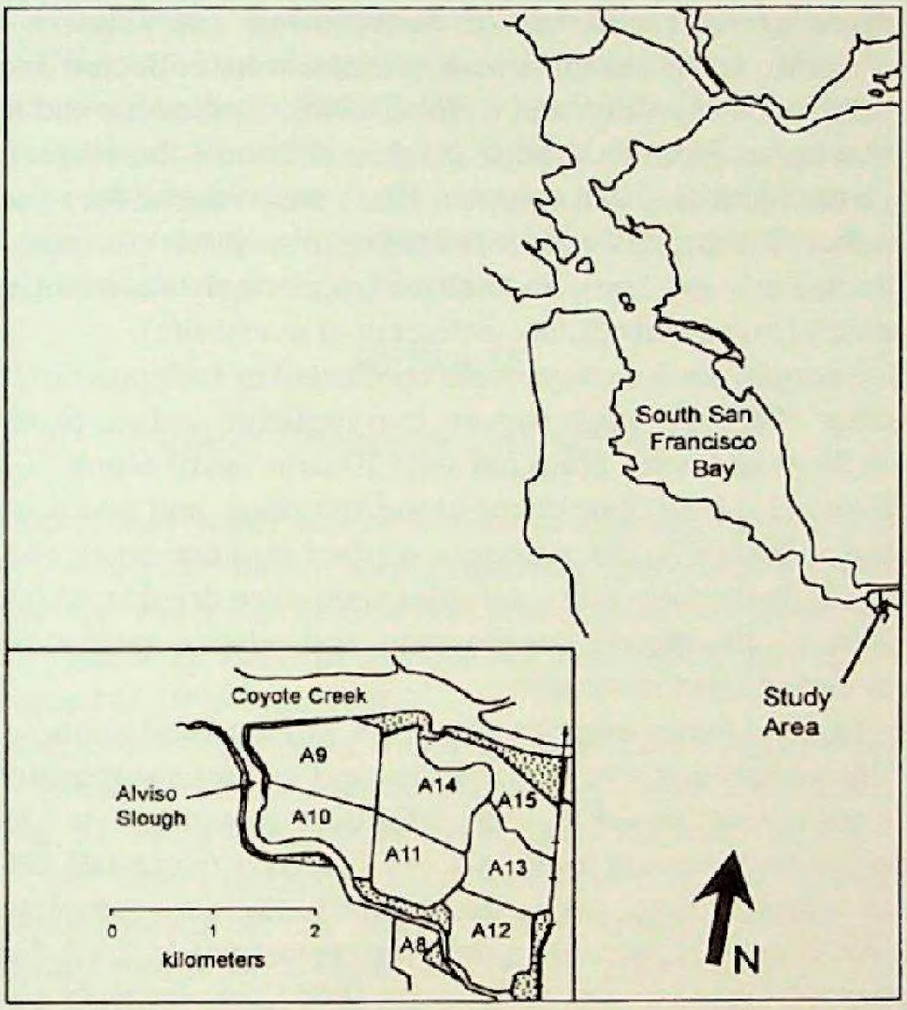

Figure 1. Study area in South San Francisco Bay. The six study ponds are A9, A10, A11, A12, A13, and A15.

1985 through April 1986 and monthly from May through October 1986. Vertical dissolved oxygen, salinity, and temperature profiles were determined for each pond in September and December 1985, in January and March 1986, and from June to September 1986.

Benthic macrophytes and planktonic algae were found in the ponds. We determined macrophyte abundance every 2-3 months between fall 1985 and fall 1986 through visual estimates of the pond surface area covered by vegetation. Relative abundance of phytoplankton was based on Secchi depth measurements obtained monthly from March through October 1986 in deep channels (<3 m) along the leeward shore of each pond. Although Secchi depths can be influenced by the presence of suspended sediments, we were confident that transparency was strongly correlated with phytoplankton abundance. First, pond sediments generally are heavily compacted and, therefore, not readily suspended (D.G. Lonzarich, pers. obs.). Moreover, Secchi depths were measured along shorelines where wind activity, which could have affected turbidity, was much reduced or absent. It was also unlikely that movement of suspended sediments from other ponds or the bay influenced Secchi depths. The lowest Secchi depths (lowest transparency) in Ponds A11-A15 were recorded in spring when water did not move among ponds. In Pond A9, Secchi measurements were made several hundred meters from the intake pipe, which often introduced turbid bay water to the ponds.

To determine general patterns of distribution and relative abundance of invertebrates, benthic and planktonic invertebrates were collected once each season, in December 1985 and May, July, and October 1986. Epibenthic and infauna samples were collected with an Eckman dredge (21.2 x 21.2 cm). Individuals retained by a 0.5-mm sieve were identified and counted. Taxa were ranked for relative abundance as either abundant (numerous and collected at every site), common (moderately abundant, collected at every site), uncommon (moderately abundant, not collected at every site), or rare (low numbers, not collected at every site).

Quantitative zooplankton surveys were conducted in each pond in January, March, July, and October 1986. For each survey, two replicate surface plankton tows were made with a 0.30-m diameter plankton net (10-µm mesh) along 50-m transects in deep-water channels (about 2 m deep) along the north and south margins of each pond. Plankton collected in the nets was washed into specimen vials and fixed in 4% formaldehyde. In the laboratory, samples were oven dried at 50-60°C for 24-48 h. Total dry weight (g), taxonomic composition, and relative species abundance were determined for each plankton sample.

We surveyed pond fishes using beach seines, gill nets, and minnow traps. Seining was effective in determining size distributions and species composition in ponds, but sampling was not always possible, especially during macrophyte blooms. Surveys were conducted in each pond at least once per season between fall 1985 and summer 1986. On each sampling date, two to three seine hauls were completed using one or two nets. For most surveys, we used a seine that measured 15.2 x 1.8 m with 0.95-cm mesh. On two occasions (January and August 1986), we also used a larger seine that measured 30.5 x 1.8 m with 0.5-cm mesh. Gill net surveys were carried out to compare patterns of abundance across ponds and seasons. In each pond, one or two nets were set for 24 h perpendicular to the pond shoreline, about 5-10 m from the bank. One net measured 36.6 x 1.8 m with two panels of 1.2 and 1.9-cm mesh; the other was 38 x 1.8 m with five panels ranging from 1.2 to 5-cm mesh. When two nets were set, they were placed along the north and south shorelines of the sampled pond. Beginning in February 1986, we used minnow traps to determine the distribution and relative abundance of fishes too small to be collected in gill nets. Because earlier seining surveys indicated that species diversity was greatest in low salinity ponds (Ponds A9 and A10), gill nets and minnow traps were set more frequently in these ponds than the others (Ponds A11-A15). Surveys were conducted monthly (Ponds A9 and A10) or bimonthly (Ponds A11-A15) between fall 1985 and fall 1986.

Relative abundance estimates were calculated for fish species collected during each survey. For species large enough to be captured in gill net surveys, relative abundance estimates were derived from the number of fish collected per 24-h effort. For remaining species, relative abundance estimates were based on the combined results of seining (catch per seine haul) and minnow trap surveys (catch per 24-h effort). Based on these results, fish were classified as abundant (>20 individuals/effort), common (6-20 individuals/effort), uncommon (1-5 individuals/effort), or rare (<1 individual/effort).

All fish (or 30 randomly selected fish in large catches) were measured ± 1 mm standard length (SL) and immediately released or sacrificed. Diets were surveyed for the most abundant species collected. Prey were identified from the stomach and anterior portion of the small intestine in each fish examined. Age and growth were estimated for some species from analyses of scales and length frequency distributions of fish collected in seine hauls. From these results, fish were classified as juveniles (age 0, <50 mm) or adults (age ≥1, ≥50 mm).

RESULTS

Water Chemistry Characteristics

During the study, bay water was diverted into Pond A9 between late spring and late fall. In 1985, water circulation was completely restored to all ponds by 17 May. In 1986, by contrast, water circulation was not restored completely until 20 June. Diversions of high salinity water from Pond A8 also varied between the 2 yr, being much more frequent in 1985 than 1986.

Based on mean monthly salinities, we identified low (<35 ppt) and high (35-90 ppt) salinity ponds. Ponds A9 and A10 were low salinity ponds and A11-A15 were high salinity ones (Fig. 2). Pond salinities varied between the two summers largely due to differences in water flow from the bay and Pond A8 (Fig. 3). Salinity differences were slight between years in the low salinity ponds; however, mean summer salinities in the high salinity ponds were significantly (20 ppt) higher in 1985 than 1986 ($t = 3.53$, $df = 29$, $P < 0.01$). Salinities were not stratified during any seasonal survey.

In addition to salinity, water quality in low and high salinity ponds differed in several other respects. Mean pH levels were generally higher and more variable in low salinity than in high salinity ponds (Fig. 3). Dissolved oxygen concentrations in low salinity ponds were more variable than concentrations in high salinity ponds, but average concentrations did not differ ($t = 1.33$, $df = 105$, $P = 0.14$) (Fig. 3). Although the ponds were shallow, both types of ponds were usually hypoxic near the bottom and vertically stratified between 0.5 and 1.0 m depth (Fig. 4). Both mean pH ($r = -0.97$, $n = 6$, $P < 0.01$) and dissolved oxygen ($r = -0.85$, $n = 6$, $P < 0.05$) were negatively correlated with mean pond salinities. As expected, dissolved oxygen concentrations were also negatively correlated with water temperature, although not significantly ($r = -0.80$, $n = 6$, $P = 0.06$).

Abiotic factors could not explain all variation in water chemistry. Dissolved oxygen concentrations and pH levels in low salinity ponds differed substantially between summer 1985 and summer 1986. In these ponds, dissolved oxygen concentrations were much higher in 1985 than in 1986 (means = 8.8 versus 5.6 mg/l; $t = 2.33$, $df = 14$, $P < 0.05$) whereas pH levels were lower (means = 8.45 versus 9.0; $t = 4.05$, $df = 14$, $P < 0.01$). Because salinities and temperatures in these ponds were relatively similar in the two summers, it is likely that other factors, such as photosynthetic activity and decomposition were responsible for differences in water quality. The only measured water quality variable not correlated with salinity was water temperature ($r = 0.14$, $n = 6$, $P > 0.50$). Pond temperatures ranged from 6 to

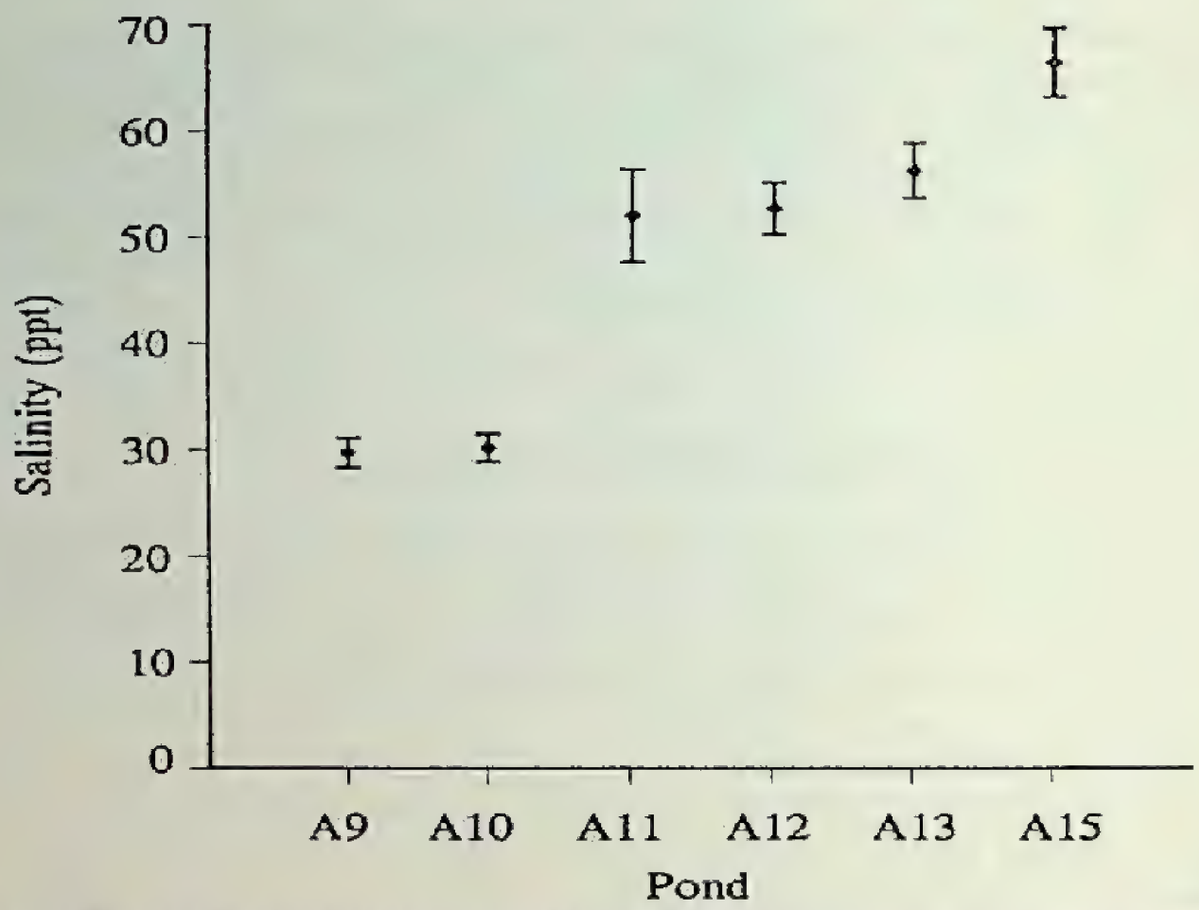

Figure 2. Mean surface water salinities (± 1 SE) in study ponds in South San Francisco Bay. From these results, ponds were identified as either low salinity (ponds A9 and A10) or high salinity ponds (A11-A15).

28°C and tracked trends in air temperature. With few exceptions, temperatures varied <2°C throughout the water column.

Phytoplankton and Macrophytic Algae

Secchi depth values were higher and more variable in low salinity than in high salinity ponds (Fig. 5). There was a sharp transition in Secchi depth values between low and high salinity ponds and phytoplankton was always the dominant primary producer in high salinity ponds. In contrast, phytoplankton and macrophytes (principally *Enteromorpha* sp.) were both common in the low salinity ponds, although their relative abundance varied inversely ($r = -0.90$, $n = 8$, $P < 0.05$). Macrophytes were most dense in Pond A9 in summer 1985 and spring 1986, but died back in summer 1986. During that time, Secchi depth values progressively decreased (Fig. 6).

Invertebrate Distributions

Benthic invertebrate species richness and zooplankton biomass varied with salinity and source of primary production. Most benthic species occurred exclusively in low salinity ponds (Table 1). In these ponds, relative abundance and species richness appeared to be strongly associated with pond macrophyte production. When pond macrophyte biomass was high in spring 1986, we collected 16 benthic and two planktonic species in low salinity ponds. The most abundant benthic species collected

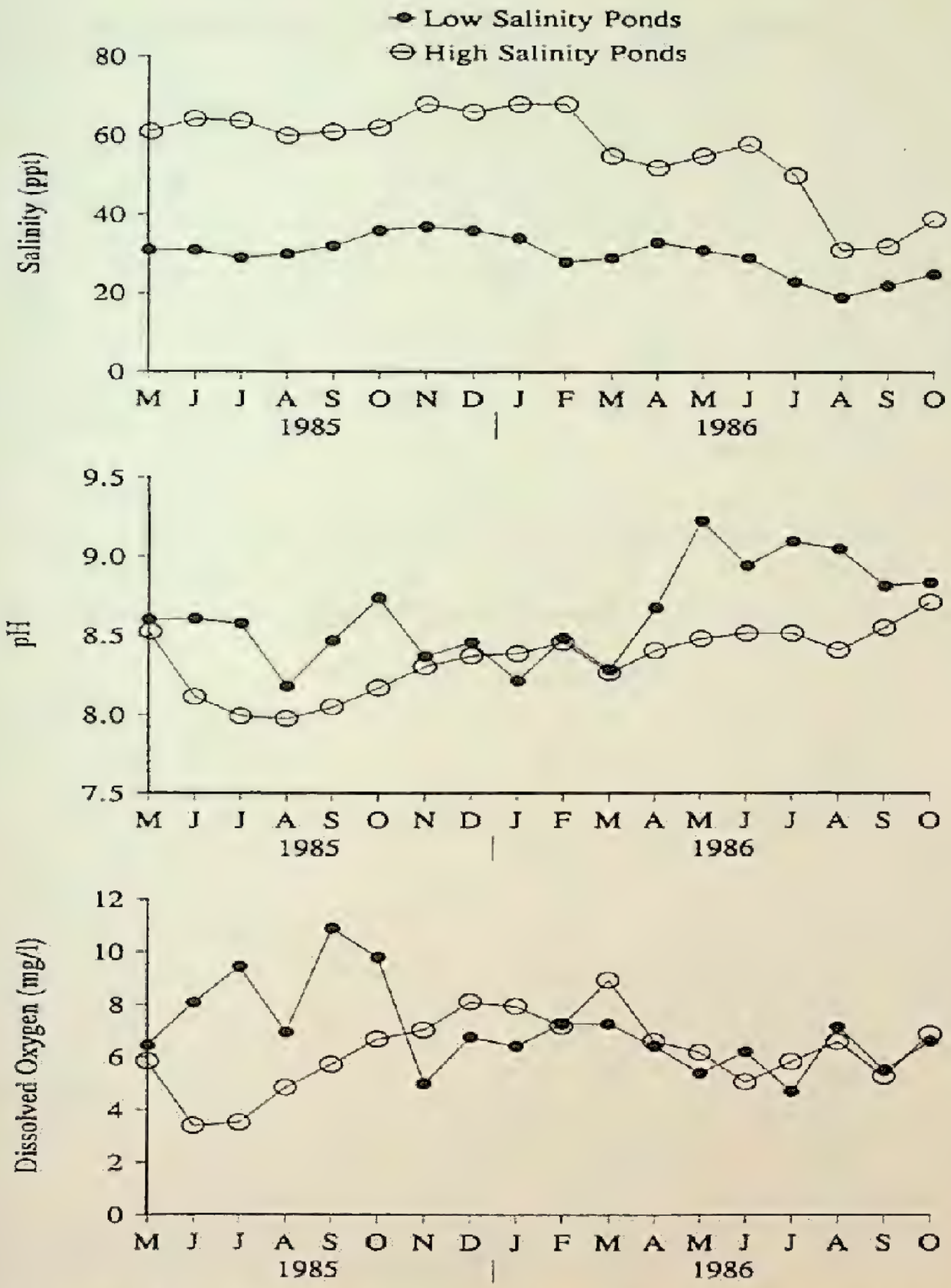

Figure 3. Seasonal variation in salinity, pH, and dissolved oxygen in low and high salinity ponds in South San Francisco Bay.

during this survey were gammarid amphipods, *Corophium* spp. and *Anisogammarus confervicolus*; the spionid polychaete, *Polydora ligni*; and oligochaetes, *Tubificoides* spp. However, during periods of reduced macrophyte cover and low oxygen concentrations in summer and fall 1986, we collected only 10 benthic and one

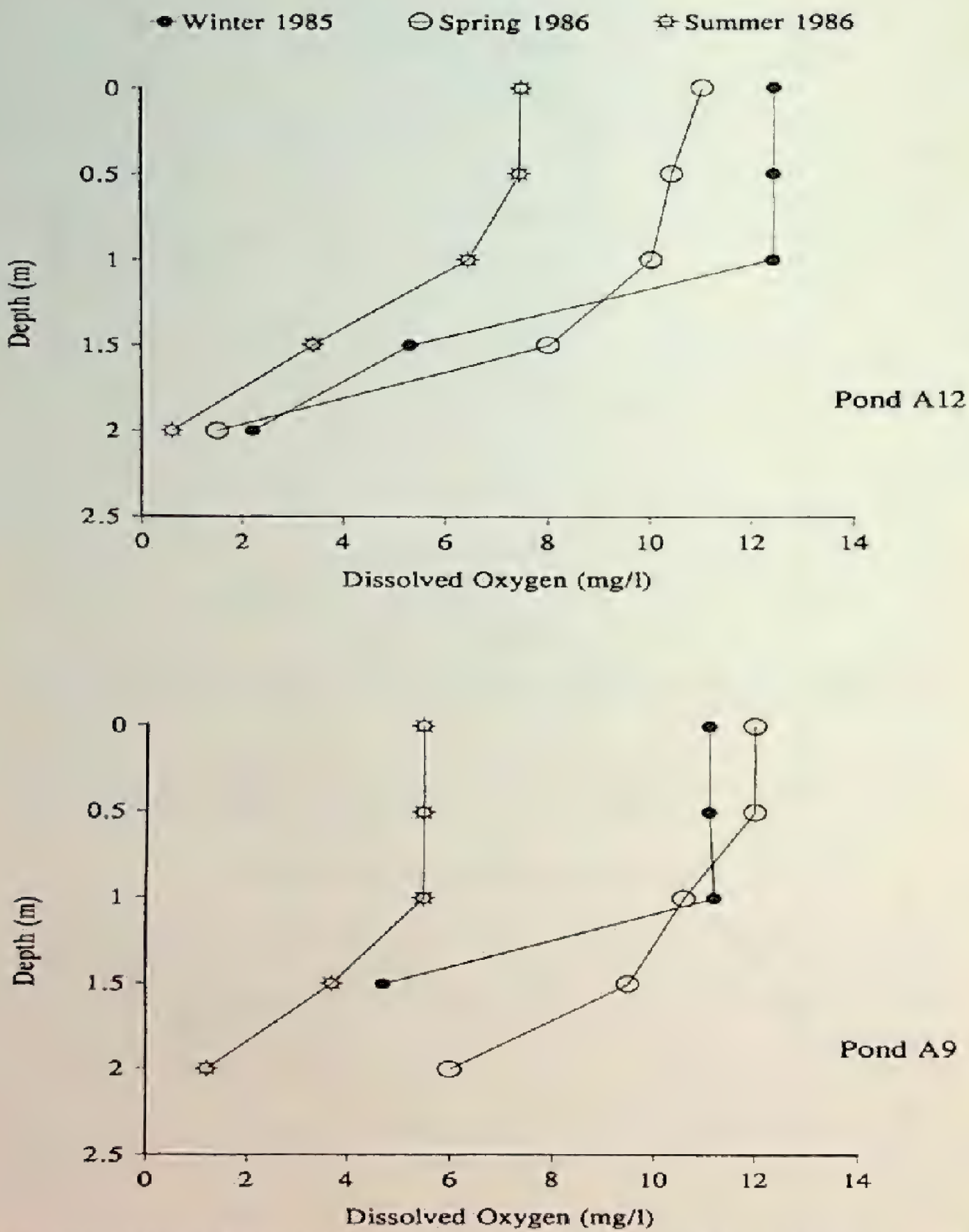

Figure 4. Seasonal dissolved oxygen profiles for Pond A9 (low salinity) and Pond A12 (high salinity) in South San Francisco Bay. Measurements were taken between 1300 and 1600 h in winter 1985 and spring and summer 1986.

planktonic species and most, with the exception of *Polydora* and *Tubificoides*, appeared to decline sharply in abundance from the spring.

The only abundant benthic and epibenthic species collected in high salinity ponds were *Polydora* and the corixid waterboatman, *Trichocorixa reticulata*. In addition

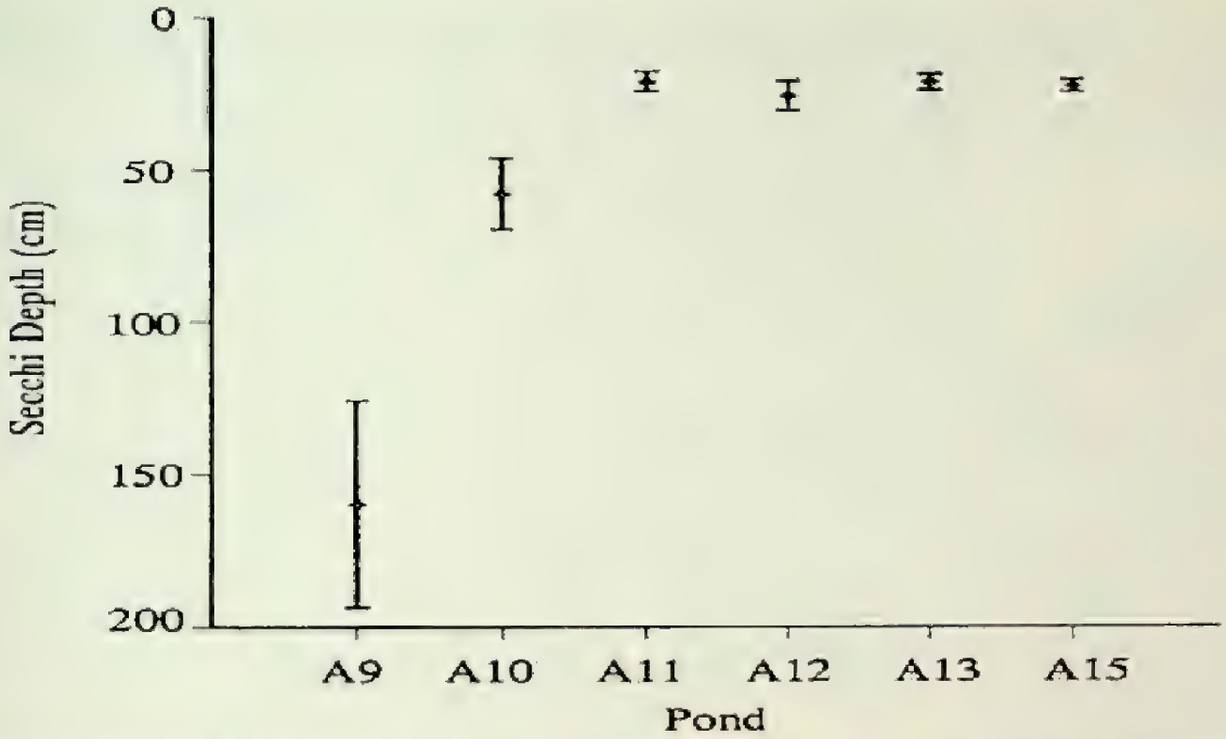

Figure 5. Mean Secchi depth (cm ± 1 SE) for the study ponds in South San Francisco Bay.

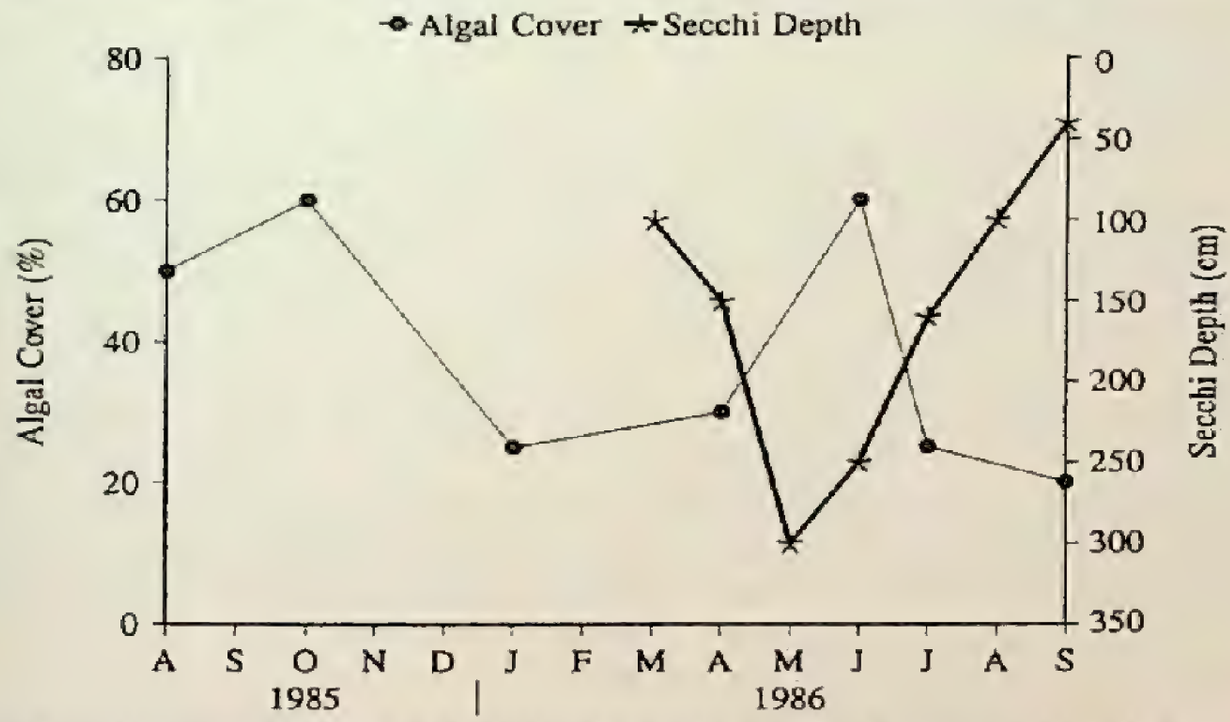

Figure 6. Algal cover as percent of pond surface area and Secchi depths for Pond A9 in South San Francisco Bay between March and October 1986.

to being common in low salinities, *Polydora* occurred in sediments from Ponds A11, A12, and A13 (to 60 ppt), whereas *Trichocorixa* was common in all high salinity ponds.

Zooplankton (calanoid copepods and brine shrimp) were abundant in high salinity ponds, but rare in low salinity ponds. In high salinity ponds, zooplankton biomass peaked in spring and summer and showed a negative correlation with Secchi depth ($r = -0.71$, $n = 9$, $P < 0.05$). Copepods and brine shrimp exhibited contrasting patterns

Table 1. Seasonal changes in distribution and relative abundance of invertebrates in low and high salinity ponds in South San Francisco Bay (winter 1985-1986 to fall 1986). a = abundant, c = common, u = uncommon, and r = rare (see text for category definitions).

	Low Salinity Ponds				High Salinity Ponds			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
CNIDARIA								
Actinaria sp.		u						
MOLLUSCA								
Gemma gemma		c						
Illyanassa obsoleta	u	c		u				
Tryonia imitator		u		c				
ANNELIDA								
Nereis succinea	u	u	u	r				
Polydora ligni		c	c		a	a	a	a
Tubificoides sp.		a	a	a				
ARTHROPODA								
Artemia salina		r	r		a	a	a	a
Anisogammarus confervicolus	u	a	c	c				
Balanus sp.		u						
Copepoda	u	u	c	c	a	a	a	a
Crangon sp.	u	u	u	u				
Corophium sp.	u	a	r	r			r	
Hemigrapsus oregonensis	u	c	r					
Ostracoda		c						
Paleomon macrodactylus	u	c	u	u				
Sphaeroma quoyana	c	c	c					
Trichocorixa reticulata		u			a	a	a	a
Total taxa	9	18	11	9	4	4	5	4

of abundance with salinity. At salinities >60 ppt, brine shrimp occurred almost exclusively, while copepods predominated at salinities <45 ppt. Between 45 and 60 ppt, both taxa were present, but neither was predictably dominant (Fig. 7).

Fishes

We collected 15 fish species in the ponds, although only three (topsmelt, *Atherinops affinis*; longjaw mudsucker, *Gillichthys mirabilis*; and rainwater killifish, *Lucania parva*) were residents in all six ponds (Table 2). Three other species (threespine stickleback, *Gasterosteus aculeatus*; yellowfin goby, *Acanthogobius flavimanus*; and Pacific staghorn sculpin, *Leptocottus armatus*) were residents in low salinity ponds and occurred at least seasonally in the high salinity ponds. The remaining nine species appeared to be seasonal immigrants from the bay, limited to salinities <35 ppt. Five of these transient species maintained populations in Pond A9 between fall 1985 and spring 1986, but none appeared in summer and fall surveys

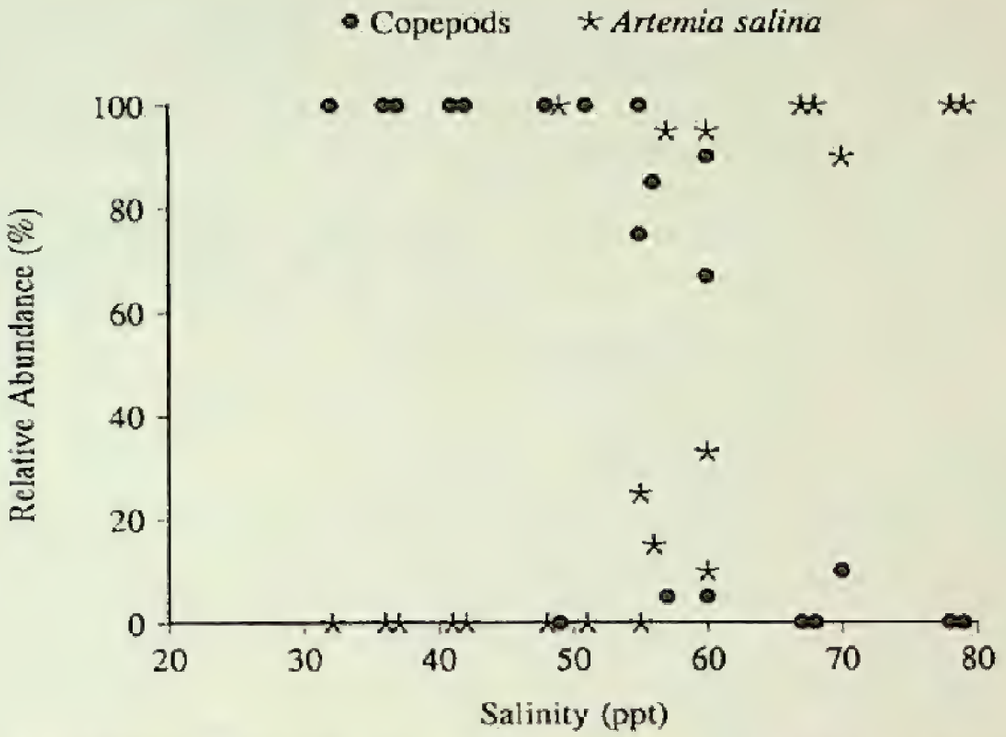

Figure 7. The relative percent abundance of copepods and brine shrimp, *Artemia salina*, in zooplankton samples collected across a range of salinities in salt evaporation ponds in South San Francisco Bay.

(Table 2). In both low and high salinity ponds, nearly all species collected experienced declines in abundance between fall 1985 and winter 1986.

Large populations of topsmelt occupied both low and high salinity ponds; however, numbers varied greatly during the study. Based on gill net results, populations in both high and low salinity ponds were highest in fall 1986 and lowest in winter (Table 2). Adults occupied all six ponds to 85 ppt, while juveniles (<30 mm) occurred in salinities to 75 ppt. Based on the presence of gravid females and larvae (<10 mm), spawning appeared to extend from February through September. In both low and high salinity ponds, individuals were 90-100 mm by the end of their 1st yr and 120-130 mm by their 2nd summer. None of the individuals collected were older than 2 yr. Topsmelt in high salinity ponds preyed on brine shrimp at very high salinities and on copepods at lower salinities (63 stomachs examined). In low salinity ponds, benthic amphipods were the primary prey through spring 1986, whereas copepods predominated in summer 1986 (22 stomachs examined).

Longjaw mudsuckers were present in all six ponds, although their relative abundance was always greatest in the high salinity ponds. Trends in relative abundance were similar to those described for topsmelt; lowest numbers were collected in gill net surveys during winter (Table 2). The presence of larvae (<10 mm) in all ponds between December and March indicated successful reproduction across a range of salinities. Based on length-frequency distributions, individuals appeared to live only 2 yr, reaching sizes of 80-100 mm in their 1st yr and 120-140 mm by their 2nd. Adults fed upon a variety of benthic (*Corophium*, *Anisogammarus*, and *Trichocorixa)* and planktonic (brine shrimp and copepods) prey (28 stomachs examined).

Table 2. Seasonal changes in the distribution and relative abundance of fishes in low and high salinity ponds in South San Francisco Bay based on results of gill net, seine, and minnow trap surveys from fall 1985 to fall 1986. Abbreviations are as follows: a = abundant, c = common, u = uncommon, and r = rare (see text for category definitions); F = fall, W = winter, Sp = spring, Su = summer; * = only juveniles present.

	Low Salinity Ponds					High Salinity Ponds				
Gill Net Surveys	F	W	Sp	Su	F	F	W	Sp	Su	F
Topsmelt, *Atherinops affinis*	a	r	c	a	a	c	u	a	a	a
Longjaw mudsucker, *Gillichthys mirabilis*	u	r	r	r	c	c	u	u	c	u
Yellowfin goby, *Acanthogobius flavimanus*	c	u	r	u	u	u		r		r
Staghorn sculpin, *Leptocottus armatus*	c	u	a	u	u			r*		
Shiner surfperch, *Cymatogaster aggregata*	c	u	r							
Leopard shark, *Triakis semifasciata*	u	u	u							
Bat ray, *Myliobatus californica*	r	r	r							
Starry flounder, *Platichthys stellatus*	r	r	r							
Northern anchovy, *Engraulis mordax*	u									
Bay goby, *Lepidogobius lepidus*	r									
English sole, *Pleuronectes vetulus*					r					
Striped bass, *Morone saxatilis*					u					
Minnow Trap and Seining Surveys										
Rainwater killifish, *Lucania parva*	a	c	c	a	u	a	u	c	c	u
Threespine stickleback, *Gasterosteus aculeatus*	u	u	u	a	u	u	r	r	c	u
Bay pipefish, *Syngnathus leptorhynchus*	r	r	r							
Species total	13	11	11	6	8	5	4	6	4	5

Rainwater killifish and threespine sticklebacks reproduced and maintained large populations in low salinity ponds, even when low dissolved oxygen concentrations severely depressed or eliminated populations of most other fishes (Table 2). Although both species occurred in high salinity ponds, populations in these ponds appeared to be much lower than those in low salinity ponds. There was no evidence of reproduction by threespine sticklebacks at high salinities. However, larval rainwater killifish were present in Ponds A12 and A13 during March 1986 (55 ppt), indicating at least limited reproductive success in high salinity ponds. The few rainwater killifish (n = 7) and threespine stickleback (n = 7) examined fed upon gammarids, brine shrimp, and copepods.

Yellowfin gobies were relatively common in low and high salinity ponds (to 50 ppt) during fall 1985, but declined thereafter (Table 2). Scale and length frequency data indicated that populations in the ponds were limited to individuals ≤2 yr old. The presence of gravid females and larvae in Pond A9 suggests that reproduction may occur in low salinity ponds. However, many of the individuals collected may have been immigrants from the bay, as numbers were low except for periods when the ponds were open to the bay. The diet of yellowfin gobies included polychaetes, oligochaetes, brine shrimp, killifish, and juvenile gobiids (14 stomachs examined).

Both adult and juvenile staghorn sculpins occurred in the ponds, although juveniles were more widespread. We collected small numbers of juveniles to 65 ppt while larger fish were limited to salinities <35 ppt. Staghorn sculpins were abundant in low salinity ponds through spring 1986, but they became scarce by midsummer (Table 2). Recently hatched juveniles inhabited Pond A9 in December 1985; however, it was unclear whether they immigrated from the bay or hatched in the ponds. The diet of staghorn sculpins in the ponds included killifish, gobies, *Crangon* spp., polychaetes, large amphipods, and brine shrimp (26 stomachs examined).

DISCUSSION

Water Quality

Water chemistry and biological characteristics of the six salt ponds indicated the presence of two major habitat types delineated largely by salinity differences. Low salinity ponds supported a greater variety of algal, invertebrate, and fish species than high salinity ponds; however, the structure of assemblages in low salinity ponds varied dramatically during the study. Seasonal fluctuations in dissolved oxygen, variation in sources of algal production, and limited opportunities for immigration were probably important causes for this variability.

The timing of surface water inputs from the bay and surrounding ponds may have influenced pond salinities and contributed significantly to variability in dissolved oxygen concentrations and pH levels. As noted previously, bay water flowed into Pond A9 between the late spring and fall; however, diversions began more than 1 month later in 1986 than in 1985. We suspect that macrophyte decomposition and subsequent poor water quality of summer 1986 in Pond A9 was due in part to the delayed influx of bay water. Elevated pH levels prior to the introduction of bay water may have reduced carbon availability (Jolliffe and Treguna 1970), although nutrient limitations and algal senescence (Carpelan 1957) also may have been important. The timing of diversions from Pond A8 into Pond A11 also varied substantially between the 2 yr, with diversions in 1985 being more frequent than in 1986. Consequently, salinities in the high salinity ponds in 1986 were as much as 40 ppt lower than during similar periods in 1985.

Primary Production and Higher Trophic Levels

Low salinity ponds supported both macrophyte and phytoplankton assemblages, but the relative abundance of these different primary producers varied during the study. Macrophytic and planktonic algae provided cover and food resources for a variety of epiphytic (e.g., *Corophium, Anisogammarus*) and planktonic invertebrate species in low salinity ponds. However, macrophyte decomposition and associated dissolved oxygen stress in summer 1986 led to declines in both fish and invertebrate diversity. Although the most common macrophyte in these ponds, *Enteromorpha*, often forms dense mats in San Francisco Bay (Josselyn and West 1985), the impact of diebacks is very pronounced in salt ponds. In salt ponds, stagnant conditions can

turn diebacks of macrophytes into major disturbances as fish become trapped in areas of oxygen depletion. In bay waters, by contrast, tides wash decomposing algae off mudflats and fish may avoid areas of oxygen depletion. In addition to the physiological stress created by low dissolved oxygen concentrations, hypoxia may have forced fish and invertebrates to oxygenated surface waters, exposing them to avian predators. During summer 1986, we observed several aggregations of terns, *Sterna* spp.; herons, Ardeidae; brown pelicans, *Pelecanus occidentalis*; gulls, *Larus* spp.; and double-crested cormorants, *Phalacrocorax auritus* (often >500 birds) feeding on fish and invertebrates in ponds A9 and A10. In contrast to low salinity ponds, high salinity ponds maintained large phytoplankton populations, but did not support significant macrophyte growth. In the absence of macrophytes, these ponds did not experience any prolonged periods of poor water quality.

Invertebrate assemblages in both low and high salinity ponds were dominated by a small number of species. In low salinity ponds, species diversity was seasonally variable, although oligochaetes were the most common taxa across all surveys. While many benthic species found in South Bay were recorded from the ponds, common bay species not encountered included a variety of infaunal molluscs and annelids (e.g., *Macoma balthica*, *Eteone californica*, *Streblospio benedicti*, *Heteromastis filiformis*) (Nichols and Thompson 1985, Hopkins 1986). The absence of these species in the ponds may have been influenced by low dissolved oxygen concentrations, though heavily compacted pond sediments also may have limited the availability of suitable habitat. Invertebrate assemblages in high salinity ponds were depauperate in comparison to low salinity ponds, but species richness was relatively stable. Of the species collected in high salinity ponds, only *Polydora ligni* was also common in low salinity ponds.

In many respects, patterns of fish distribution in the ponds paralleled those for invertebrates. Assemblages in low salinity ponds varied greatly over the study, although topsmelt and rainwater killifish typically were the most abundant species collected. Topsmelt also are very abundant in South Bay (Lonzarich and Hobson[6] 1988), but some common bay species (e.g., brown smoothhound, *Mustelus henlei*, and Pacific herring, *Clupea harengus*) were absent from the ponds and others (e.g., shiner surfperch, *Cymatogaster aggregata*; northern anchovy, *Engraulis mordax*; and bat ray, *Myliobatis californica*) were probably much less common in the ponds than the bay (Armor and Herrgesell 1985, Lonzarich and Hobson[6] 1988). The disappearance of seasonal residents from low salinity ponds in summer 1986 may have been associated with poor water quality or changing habitat requirements with age. The occurrence of these transient species in the ponds will likely depend strongly on suitable water quality and the timing of water inputs from the surrounding bay.

Along with these seasonal changes in diversity, fishes in both low and high salinity ponds experienced large fluctuations in abundance during the study. Most significant were the population declines of winter 1986. Because fish cannot emigrate from the

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[6] Lonzarich, D.G. and K. Hobson. 1988. A biological survey of fish and invertebrate use of Plummer Creek, South San Francisco Bay, California, 1986-87. Report to the U.S. Fish and Wildlife Service.

ponds, mortality and the lack of bay immigrants following the closure of the Pond A9 intake pipe were probably the most important causes for these declines.

Fishes resident in the ponds shared several characteristics. In addition to their tolerance of a broad range of water quality conditions, these species are short-lived (≤2 yr), small (<150 mm), and diet generalists. Adults and juveniles of the most common fishes consumed benthic (*Trichocorixa*, *Polydora*) and planktonic (*Artemia* and copepods) prey. The lifespan of at least one pond resident may be short compared with populations elsewhere. Topsmelt live more than 5 yr in estuaries and reach sizes >180 mm (Schultz 1933). Although not as long-lived as estuarine populations, topsmelt in low and high salinity ponds grew at rates comparable to fish of the same age in other systems (Schultz 1933, Horn 1980).

Salt ponds have long been recognized as important habitats for migratory waterbirds (Anderson 1970, Gill 1977, Takekawa et al.[3] 1988) but, with the exception of one study by Carpelan (1957), characteristics of pond aquatic communities have been poorly understood. For hypersaline ponds (>35 ppt), the results of this study are consistent with those of Carpelan (1957). Further, our study also has shown that low salinity salt ponds maintain diverse, though unstable, animal assemblages, which in several respects are distinct from those in surrounding bay waters. Salinity plays a very important role in shaping the structure of pond communities, although it appears that poor water quality also can have profound effects on pond biology, especially since fishes and invertebrates are restricted to the ponds during these periods. Closure of ponds to tidal flow creates stagnant conditions, which can lead to macrophyte decomposition and poor water quality. Further, seasonal closure of these ponds to tidal flow prevents movement of fishes between the ponds and the bay.

ACKNOWLEDGMENTS

We extend special thanks to D. Clanon, V. Layne, C. Pelles, M. Robinson, J. Vandermere, and P. Woodin for help with field and laboratory work. We also are grateful to the Santa Clara Audubon Society for a generous grant and the Don Edwards San Francisco Bay National Wildlife Refuge and the Cargill Leslie Salt Company for providing access to their land. Data on pond water depth and movement were provided by the Cargill Leslie Salt Company.

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Received: 15 July 1996
Accepted: 16 July 1997

California Fish and Game 83(3):105-117 1997

PREVALENCE, RELATIVE ABUNDANCE, AND MEAN INTENSITY OF PLEROCERCOIDS OF *PROTEOCEPHALUS* SP. IN YOUNG STRIPED BASS IN THE SACRAMENTO-SAN JOAQUIN ESTUARY

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Up to 79% of larval and juvenile striped bass, *Morone saxatilis*, in the Sacramento-San Joaquin Estuary harbor plerocercoids tentatively identified as *Proteocephalus* sp. Histological slides of infected striped bass revealed cysts encapsulating plerocercoids but no other host reaction. Prevalence of plerocercoids varied significantly among years and increased with striped bass length. Two copepods, *Sinocalanus doerri* and *Eurytemora affinis*, eaten by striped bass harbor a procercoid and are probable vectors. However, copepod abundance in the estuary and in the diet of striped bass was not consistently correlated with prevalence of plerocercoids in striped bass. Plerocercoid prevalence correlated significantly with water temperature and transparency but not with river outflow or electrical conductivity.

INTRODUCTION

The population size of the striped bass, *Morone saxatilis*, an important sport fish in the Sacramento-San Joaquin Estuary, has declined over the past three decades (Stevens et al. 1985). California Department of Fish and Game (CDFG) biologists attribute the bass decline mainly to entrainment losses of young striped bass at water diversions and subsequent reduced recruitment to the adult stock and decreased egg production (Stevens et al. 1985, CDFG[1] 1992). Other factors, such as parasitism, may also contribute to annual variation in year class size.

Effects of parasitism on a population can range from negligible to extremely detrimental depending on the intensity of infection and the physiological effects of the parasite on its host. Parasites may reduce fecundity, increase energetic demands, decrease host lifetime reproductive rate, and reduce survival (Needham and Behnke 1965, Schwartz and Cameron 1993, Weissman et al. 1993). Although parasitism

[1] CDFG. 1992. A re-examination of factors affecting striped bass in the Sacramento-San Joaquin Estuary. WRINT-DFG-Exhibit 2. Written testimony by the California Department of Fish and Game for the State Water Resources Control Board 1992 Water Rights Phase of the Bay-Delta Estuary Proceedings.

may combine with other stressors to limit a host population, it is often ignored as a possible population regulatory force (Scott and Dobson 1989, Holmes 1996).

Several types of cestodes have been found in striped bass from the Sacramento-San Joaquin Estuary (Love and Moser[2] 1983), including plerocercoids of the family Tetraphyllidae in young fish (Moser et al.[3] 1985) and *Lacistorhynchus dollfusi* (Lacistorhychidae) in adults (Sakanari and Moser 1990). In laboratory experiments, striped bass ingesting copepods infected with *L. dollfusi* procercoids became infected with plerocercoids (Sakanari and Moser 1986). Also, two types of *Proteocephalus* sp. larvae, a proteocephalid, and *Scolex pleuronectis*, a tetraphyllid, have been reported from young striped bass in Chesapeake Bay (Paperna and Zwerner 1976). Histopathological damage from *Proteocephalus ambloplitis* infection has been reported in largemouth bass, *Micropterus salmoides*; spotted bass, *Micropterus punctulatus* (Joy and Madan 1989); smallmouth bass, *Micropterus dolomieui* (Esch and Huffines 1973); and bluegill, *Lepomis macrochirus* (Bailey 1983).

Two calanoid copepods, *Sinocalanus doerri* and *Eurytemora affinis*, that are prominent in the diet of young striped bass in the Sacramento-San Joaquin Estuary harbor procercoids and are, thus, possible vectors for the apparent *Proteocephalus* sp. plerocercoid in young striped bass. Generally, proteocephalids develop from an egg stage into a free living ciliated embryo, a coracidium. After ingestion by a zooplankter, the coracidium develops into a procercoid. When an infected zooplankter is eaten by a fish, the procercoid develops into a plerocercoid in the intestinal wall. A reproductive adult then forms and begins producing eggs that are discharged with feces (Chandler and Read 1961).

We examined the annual occurrence and distribution relative to environmental factors of plerocercoids in young striped bass and the distribution of two potential vectors, *S. doerri* and *E. affinis*. This work was an outgrowth of the incidental discovery of these parasites during a study of young striped bass diet.

METHODS

Striped bass were collected by three methods:

1) Larvae and post-larvae were collected with a 500-µm mesh ichthyoplankton net mounted on an epibenthic sled during the routine CDFG egg and larva survey (ELS). Tissues were examined from 29,982 fish collected at 18 sites sampled every 4th d from mid-April to July during the 1986 and 1988-1993 surveys. These fish ranged from 3 to 47 mm standard length (SL). From a special study at one site in 1987, we examined 345 larval striped bass ranging from 5 to 39 mm SL. Zooplankton samples were collected concurrently with egg and larva samples with

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[2] Love, M.S. and M. Moser. 1983. A checklist of parasites of California, Oregon, and Washington marine and estuarine fishes. NOAA Technical Report NMFS SSRF-777.

[3] Moser, M., J.A. Sakanari, C.A. Reilly, and J. Whipple. 1985. Prevalence, intensity, and persistence of *Anisakis* sp. larvae and *Lacistorhynchus tenuis* metacestodes in San Francisco striped bass. NOAA Technical Report NMFS 29.

a 150-µm-mesh (No. 10) Clarke-Bumpus net. *Sinocalanus doerri*, *E. affinis*, and other species were identified and counted. Water temperature, transparency (Secchi disc), and surface electrical conductivity (EC) were measured at each site. Freshwater flow through the estuary was also explored as a possible factor affecting plerocercoid abundance and distribution. The California Department of Water Resources DAYFLOW database supplied estimates of flow at three locations: Sacramento-San Joaquin Delta outflow at Chipps Island, Jersey Point on the lower San Joaquin River, and Freeport on the Sacramento River.

2) Larger young striped bass were collected from 1987 to 1993 during a summer CDFG townet survey (TNS) (Stevens 1977) using a 13-mm stretch mesh net with a 3.2-mm bobbinet cod end mounted on an epibenthic sled. Thirty sites from San Pablo Bay upstream through the Sacramento-San Joaquin Delta were surveyed biweekly beginning in June and ending in July. We examined tissues from 4,894 of these fish ranging from 6 to 102 mm fork length (FL).

3) To determine if plerocercoids persist in older juveniles, we examined 110 striped bass collected in December 1993 in the CDFG midwater trawl survey (MWT) using a net with 13-mm cod end mesh and a 3.7 x 3.7-m mouth. These striped bass ranged from 58 to 135 mm FL. *Sinocalanus doerri* from their stomachs were examined for procercoids.

We analyzed the relationship between plerocercoid prevalence and year, time of year, fish length, and sampling area using ANOVA and Tukey tests (SAS Institute Inc. 1988). Chi-square analysis of differences in prevalence between years was performed using MINITAB (Minitab Inc. 1994). Plots (S-PLUS) of physical factors were created using a general additive model with the contribution of each individual physical factor (log effect) to the prevalence of plerocercoids plotted with approximate 95% confidence bounds about each fitted curve (Hastie and Tibshirani 1990). Whenever possible, data from the ELS and TNS were combined for analysis, but the method of data collection prevented grouping in all instances. Egg and larva survey standard lengths were converted to fork lengths when data were combined. Fish from the ELS were grouped by year and length while TNS fish were collected by area and year and could not be combined with each other for correlations with water parameters and flow.

The terms used in this paper for parasite infection are from Margolis et al. (1982). Prevalence is the percent of striped bass examined that were infected with plerocercoids. Relative abundance is the mean number of plerocercoids found per striped bass sampled. Mean intensity is the mean number of plerocercoids found per infected striped bass.

RESULTS

Plerocercoids were found encysted in the mesenteries and stomachs of striped bass, but no other host response was observed (Fig. 1). Parasite infestation rates varied with year, survey, and fish length. The greatest prevalence of plerocercoids in the ELS occurred in 1987 when 72% of striped bass were infected, but these results may not be representative of the population because only one sample was

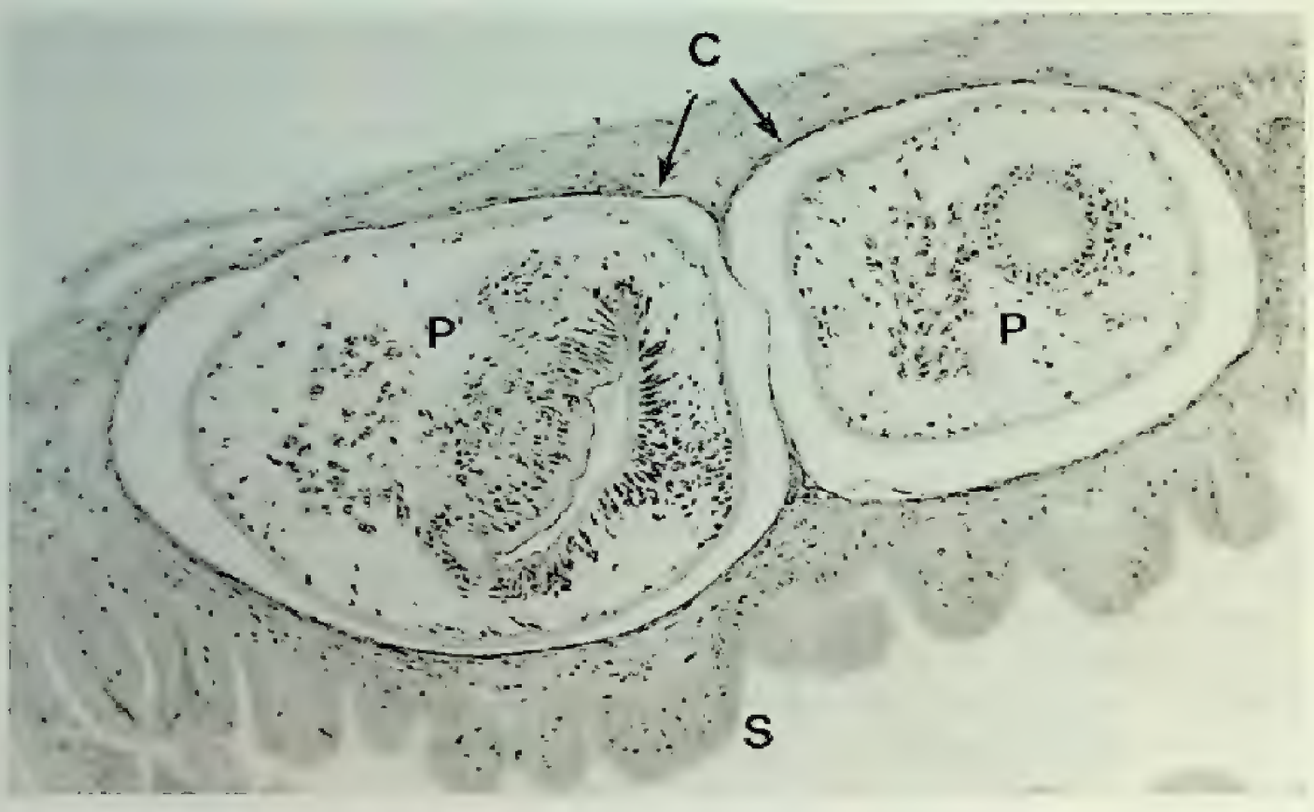

Figure 1. Section of striped bass stomach (S), stained using a hematoxylin and eosin counterstain, showing two plerocercoids (P) encysted (C) by the host. Photograph by the senior author.

collected that year. Prevalence ($\chi^2 = 1037$, df = 6, $P < 0.001$), relative abundance ($F = 52.0$; df = 1, 6; $P < 0.001$), and mean intensity ($F = 4.0$; df = 1, 6; $P < 0.001$) varied significantly among years. Relative abundance of parasite infestation in striped bass from the ELS was significantly greater in 1988 than in other years (Tukey's test, $P < 0.001$), while mean intensity was significantly greater in 1992 than all years except 1988 (Tukey's test, $P < 0.001$) (Table 1). Chi-square tests indicated that in all years the prevalence of plerocercoids was significantly greater in fish collected in the TNS than in the ELS (all $P < 0.001$). Prevalence ($\chi^2 = 885$, df = 6, $P < 0.001$), relative abundance ($F = 192$; df = 1, 6; $P < 0.001$), and mean intensity ($F = 115$; df = 1, 6; $P = 0.001$) of plerocercoids in TNS striped bass varied significantly among years (Table 1). Relative abundance and mean intensity of plerocercoids in TNS fish were significantly higher in 1987 than in any other year (Tukey's tests, $P < 0.05$). Striped bass collected by the MWT in 1993 had the highest prevalence of any sample (79%) (Table 1). All measures of infestation for the MWT samples were greater than for either the ELS or TNS samples in 1993. However, the relative abundance and mean intensity of plerocercoids were greater in 1987 for TNS fish than for MWT fish in 1993. The maximum number of parasites found in an infected fish ranged from five in the 1993 ELS to 432 in the 1987 TNS.

Within years and surveys, parasite prevalence was inconsistently related to water quality parameters. For ELS fish, plerocercoid prevalence correlated significantly ($P < 0.05$) with temperature in all years except 1992, but only in a few years with transparency and EC (Table 2). Plerocercoid abundance increased with temperature and increased slightly at high transparency but exhibited no trend with EC (Fig. 2).

Table 1. Annual means for prevalence, relative abundance, mean intensity, and annual range in numbers of plerocercoids in young striped bass from three surveys in the Sacramento-San Joaquin Estuary. N = the total number of fish sampled. Superscript letters represent Tukey's groupings; means with the same letter are not significantly different. In the egg and larva survey, no statistics were performed on 1987 data because only one site was sampled. ID = insufficient data.

Year	Prevalence	Relative abundance	Mean intensity	Range	N
		Egg and larva survey			
1986	8	0.15^{B}	1.8^{BC}	0-7	1,261
1987	ID	ID	ID	ID	ID
1988	12	0.36^{A}	3.0^{AB}	0-29	3,324
1989	2	0.06^{CD}	2.1^{BC}	0-30	9,527
1990	1	0.03^{DE}	1.8^{BC}	0-7	4,442
1991	4	$0.07B^{CDE}$	1.6^{C}	0-7	2,650
1992	2	0.10^{BC}	4.3^{A}	0-6	2,714
1993	1	0.01^{DE}	1.8^{BC}	0-5	6,064
		Townet survey			
1987	48	20.0^{A}	41.4^{A}	0-432	1,146
1988	64	4.6^{C}	7.1^{C}	0-47	822
1989	14	0.8^{C}	5.4^{C}	0-25	515
1990	13	0.5^{C}	4.2^{C}	0-23	600
1991	40	2.8^{C}	7.0^{C}	0-82	661
1992	67	12.5^{B}	18.9^{B}	0-210	1,152
1993	60	4.5^{C}	7.5^{C}	0-156	1,528
		Midwater trawl survey			
1993	79	18.1	22.8	0-179	110

Table 2. Correlations of plerocercoid prevalence in striped bass from the egg and larva survey (ELS) and townet survey (TNS) in the Sacramento-San Joaquin Estuarywith temperature, electrical conductivity (EC), and water transparency (Secchi). No TNS data (ND) was collected in 1986 and there was insufficient data (ID) for a correlation with the 1987 ELS. $*P < 0.05$, $**P < 0.01$.

	Egg and larva survey			Townet survey		
Year	Temperature	EC	Secchi	Temperature	EC	Secchi
1986	0.59**	0.35*	-0.33	ND	ND	ND
1987	ID	ID	ID	0.06	-0.60	0.53**
1988	0.47**	-0.16	0.26*	0.03	0.16	-0.07
1989	0.39**	-0.08	-0.12	-0.15	0.09	0.07
1990	0.37**	-0.13	0.20*	-0.24	0.29	-0.06
1991	0.38**	-0.03	-0.01	0.13	0.24	-0.34
1992	0.15	0.21*	-0.17	0.33**	-0.20	0.49**
1993	0.19*	0.38*	-0.10	-0.05	0.02	-0.002

In contrast, plerocercoid prevalence in TNS fish did not consistently correlate significantly with water quality variables. Temperature was correlated with parasite prevalence only in 1992, and Secchi readings correlated with parasite prevalence in

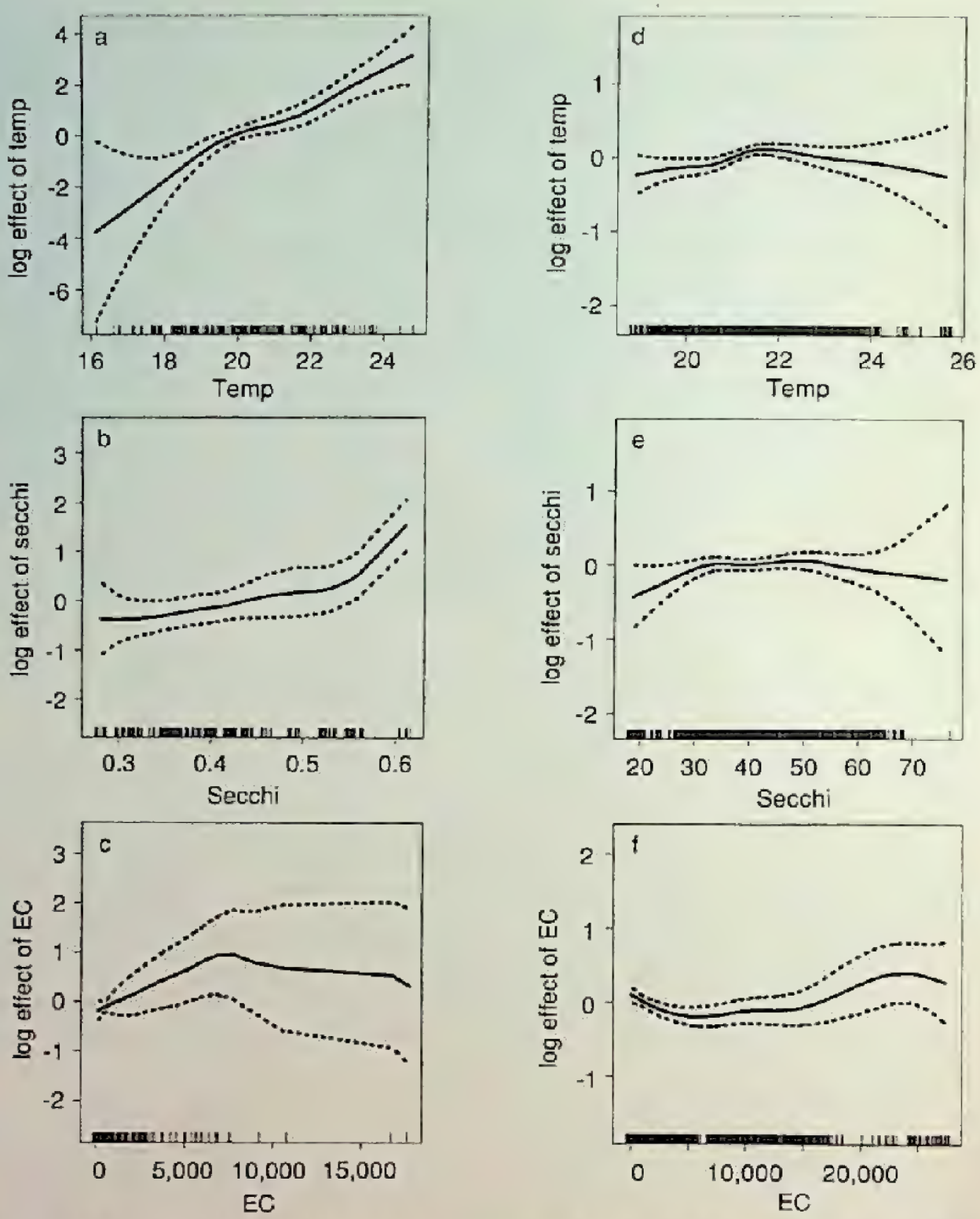

Figure 2. Plots of the log of relative contribution to plerocercoid prevalence in young striped bass from the Sacramento-San Joaquin Estuary by the smooth function of (a) temperature, (b) transparency, and (c) electrical conductivity (EC) in the egg and larva survey. Plots of the log of relative contribution to plerocercoid prevalence by the smooth function of (d) temperature, (e) transparency, and (f) EC in the townet survey.

1987 and 1992 (Table 2). Parasite prevalence was not correlated with EC. Plerocercoid prevalence in the ELS increased with temperature and at high Secchi disc readings, but showed no relationship with EC (Fig. 2) and no effect of water quality measurements was found on plerocercoid prevalence in TNS fish.

Plerocercoid prevalence increased with increasing fish length in all years in the ELS and TNS (Fig. 3). In 1993, which had data for all three surveys, mean intensity of plerocercoids increased with fish length until becoming asymptotic at approximately 62 mm (Fig. 4).

For ELS and TNS striped bass, prevalence and intensity of plerocercoid infection were not significantly correlated ($P > 0.05$) with any of the flow variables, but correlations between these measures of infestation and Sacramento River flow were generally negative (Table 3).

Only in 1989 was the prevalence of plerocercoids significantly and positively correlated ($P < 0.05$) with the number of *S. doerri* in the diet of ELS fish (Table 4); other years had negative but nonsignificant correlations. Plerocercoid prevalence was significantly positively correlated ($P < 0.05$) with *E. affinis* in the diet of ELS fish in 1992, but significantly negatively correlated ($P < 0.05$) in 1988. For TNS fish, parasite prevalence was not significantly correlated with either *S. doerri* or *E. affinis* in the diet of striped bass in any year (Table 4).

Correlations between prevalence of plerocercoids in striped bass and abundance of *S. doerri* and *E. affinis* in the estuary were also inconsistent (Table 5). Statistically significant correlations for *S. doerri* occurred in 1989 ($P < 0.05$) and 1991 ($P < 0.01$) and for *E. affinis* only in 1986 ($P < 0.01$). Nevertheless, these copepods harbor procercoids (Fig. 5).

DISCUSSION

The identity of plerocercoids found in striped bass in the Sacramento-San Joaquin Estuary is uncertain. C. Alexander (San Francisco State University) tentatively identified plerocercoids from our study as *Proteocephalus* sp., while Moser et al.[3] (1985) identified plerocercoids from Sacramento-San Joaquin Estuary striped bass as tetraphyllids. This confusion may have occurred because both tetraphyllids and *Proteocephalus* are characterized by having four scolices. Tetraphyllids typically parasitize elasmobranchs (Chandler and Read 1961) and are unlikely to be found upstream where young striped bass probably become infected. Conversely, the definitive host of *Proteocephalus* sp. is likely to be a freshwater fish. Indeed, *Proteocephalus* sp. has been found encysted in the mesenteries of white catfish, *Ameiurus catus*, in the Sacramento-San Joaquin Delta (Edwards and Nahhas 1968) and San Francisco State University students have collected three species of *Proteocephalus* from three species of catfish in the delta (C. Alexander, pers. comm.). Because we could not identify *Proteocephalus* to species, we could not determine its life cycle, vectors, and definitive host.

Adult striped bass are often infected with an incompatible elasmobranch parasite, *L. dollfusi*, which burrows through the bass intestines, dies, and becomes encysted. Multiple parasites are encapsulated to form a raft which is shed through the abdominal wall, causing a lesion (Hensley and Nahhas 1975, Moser et al. 1984). *Proteocephalus* sp. plerocercoids found in young striped bass may have a similar incompatibility with their host, as they have not been found in adult striped bass (M. Moser, University of California, Santa Cruz, pers. comm.). Similarly,

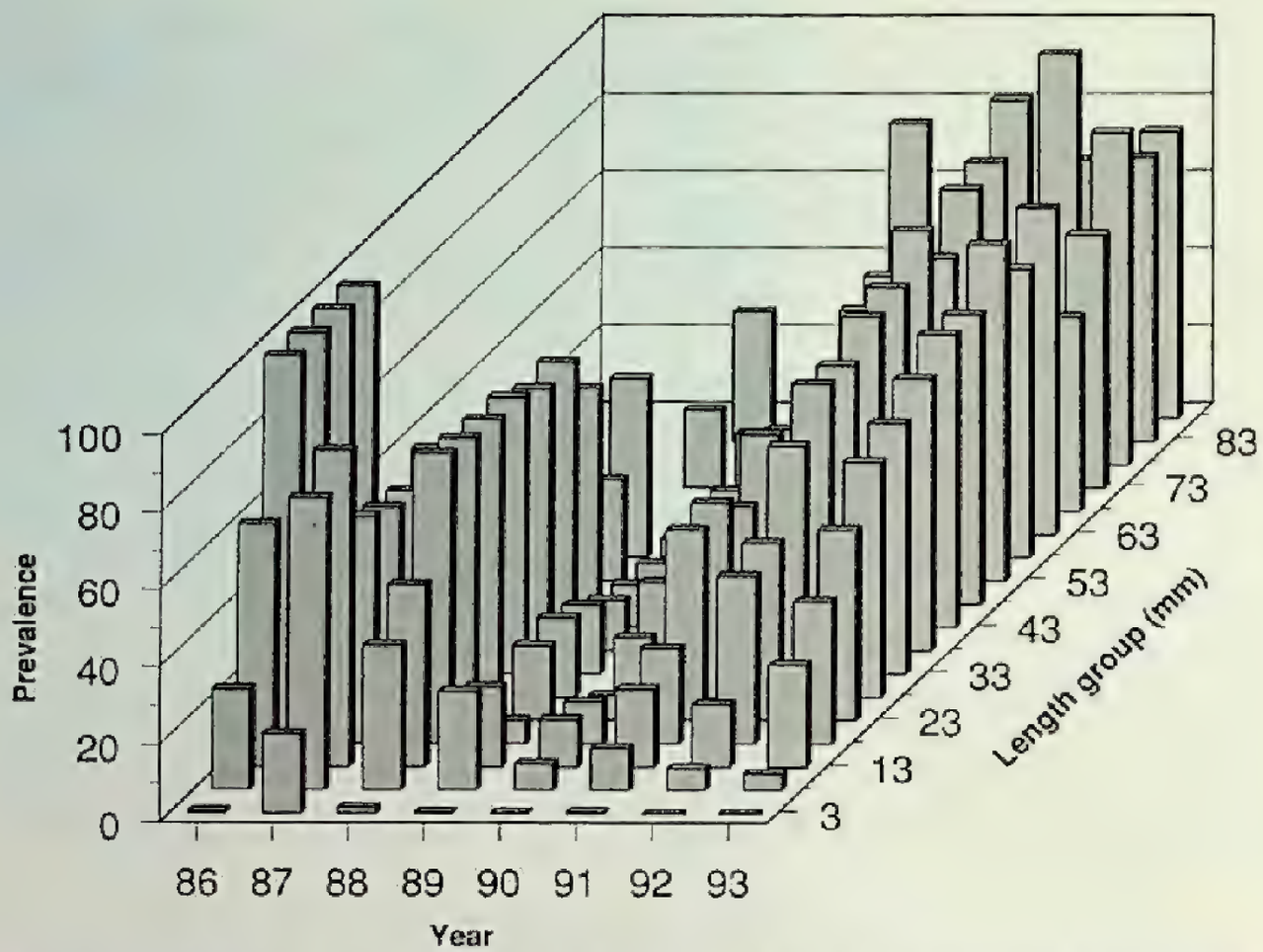

Figure 3. Prevalence of plerocercoids in striped bass by year and length from the combined egg and larva and townet surveys in the Sacramento-San Joaquin Estuary.

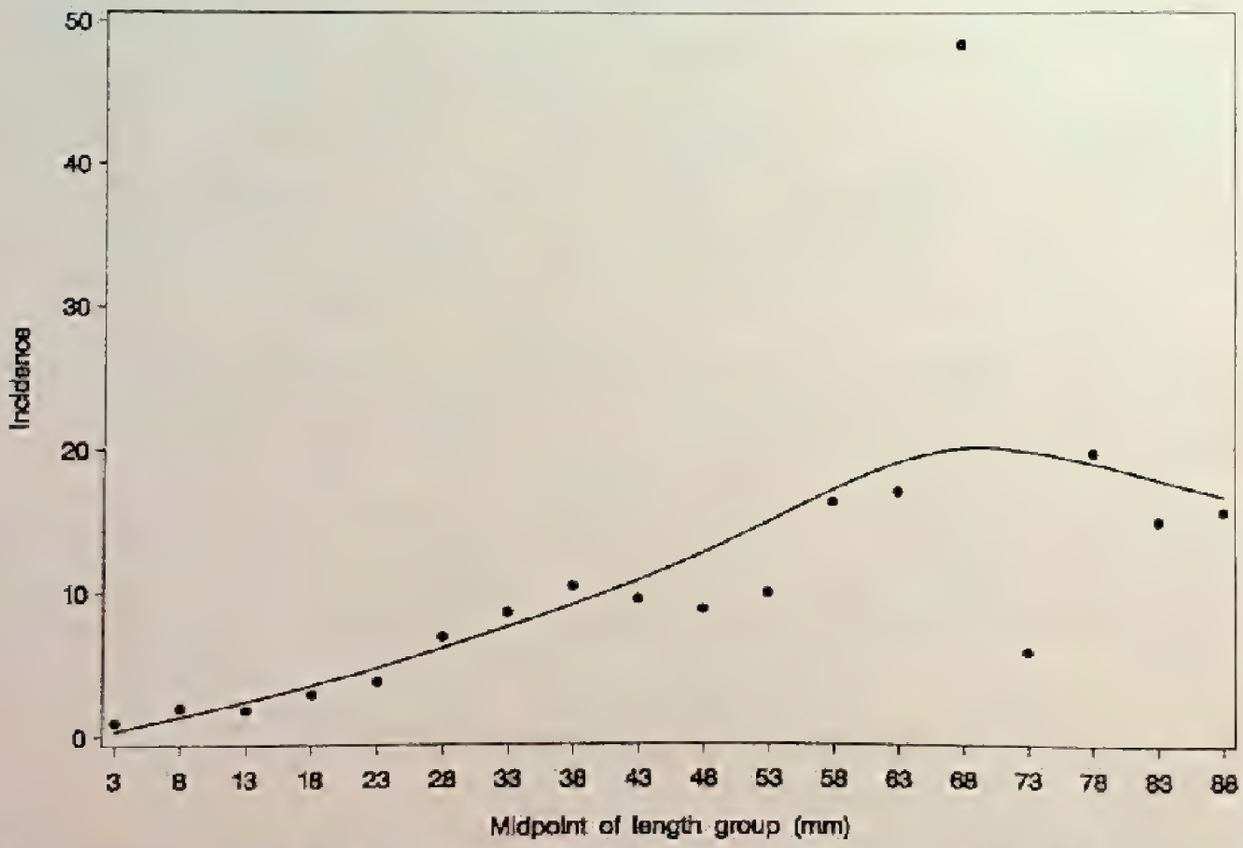

Figure 4. Regression of Sacramento-San Joaquin Estuary egg and larva survey, townet survey, and midwater trawl survey plerocercoid mean intensity on striped bass fork length in 1993.

Table 3. Correlation coefficients for annual prevalence and mean intensity of plerocercoid infestations in larval (egg and larva survey) and juvenile (townet survey) striped bass versus Sacramento-San Joaquin Delta outflow, prevalence and mean intensity in San Joaquin River fish versus flow at Jersey Point on the lower San Joaquin River, and prevalence and mean intensity in Sacramento River fish versus Sacramento River flow. All coefficients are nonsignificant ($P>0.05$).

	Larval striped bass		Juvenile striped bass	
Flow type	Prevalence	Mean intensity	Prevalence	Mean intensity
Delta outflow	0.07	-0.44	0.21	0.25
Flow at Jersey Point	0.04	-0.46	-0.13	0.35
Sacramento River flow	-0.57	-0.39	-0.19	0.07

Table 4. Correlation coefficients for plerocercoid prevalence in larval (egg and larva survey [ELS]) and juvenile (townet survey [TNS]) striped bass in the Sacramento-San Joaquin Estuary versus copepods in stomach contents. Data from the ELS in 1987 could not be used in this analysis (ND) and data were insufficient (ID) in 1990. In the TNS, not enough *E. affinis* was consumed by sampled fish for correlations analysis in 3 of the 6 yr (ID). * $P<0.05$.

	Larval striped bass		Juvenile striped bass	
Year	*S. doerri*	*E. affinis*	*S. doerri*	*E. affinis*
1987	ND	ND	0.06	<0.01
1988	-0.27	-0.30*	0.04	-0.04
1989	0.33*	-0.07	-0.03	ID
1990	ID	-0.19	0.02	ID
1991	-0.12	-0.20	0.03	0.06
1992	-0.17	0.34*	0.06	ID

Table 5. Correlation coefficients for plerocercoid prevalence in larval striped bass (egg and larva survey) from the Sacramento-San Joaquin Estuary versus *S. doerri* and *E. affinis* abundance. No zooplankton (ND) was collected in 1987. * $P<0.05$, ** $P<0.01$.

Year	*S. doerri*	*E. affinis*
1986	0.12	0.60**
1987	ND	ND
1988	0.08	-0.09
1989	0.16*	-0.13
1990	0.05	-0.12
1991	0.38**	-0.05
1992	ND	ND
1993	-0.02	-0.14

Proteocephalus type A was in 76% and *Proteocephalus* type B in 46% of young-of-the-year (YOY) striped bass mesenteries from Chesapeake Bay, but they did not infect fish more than 1 yr old (Paperna and Zwerner 1976).

Laboratory experiments indicated that striped bass from the Sacramento-San Joaquin Estuary have greater immunity to *L. dollfusi* than East Coast striped bass

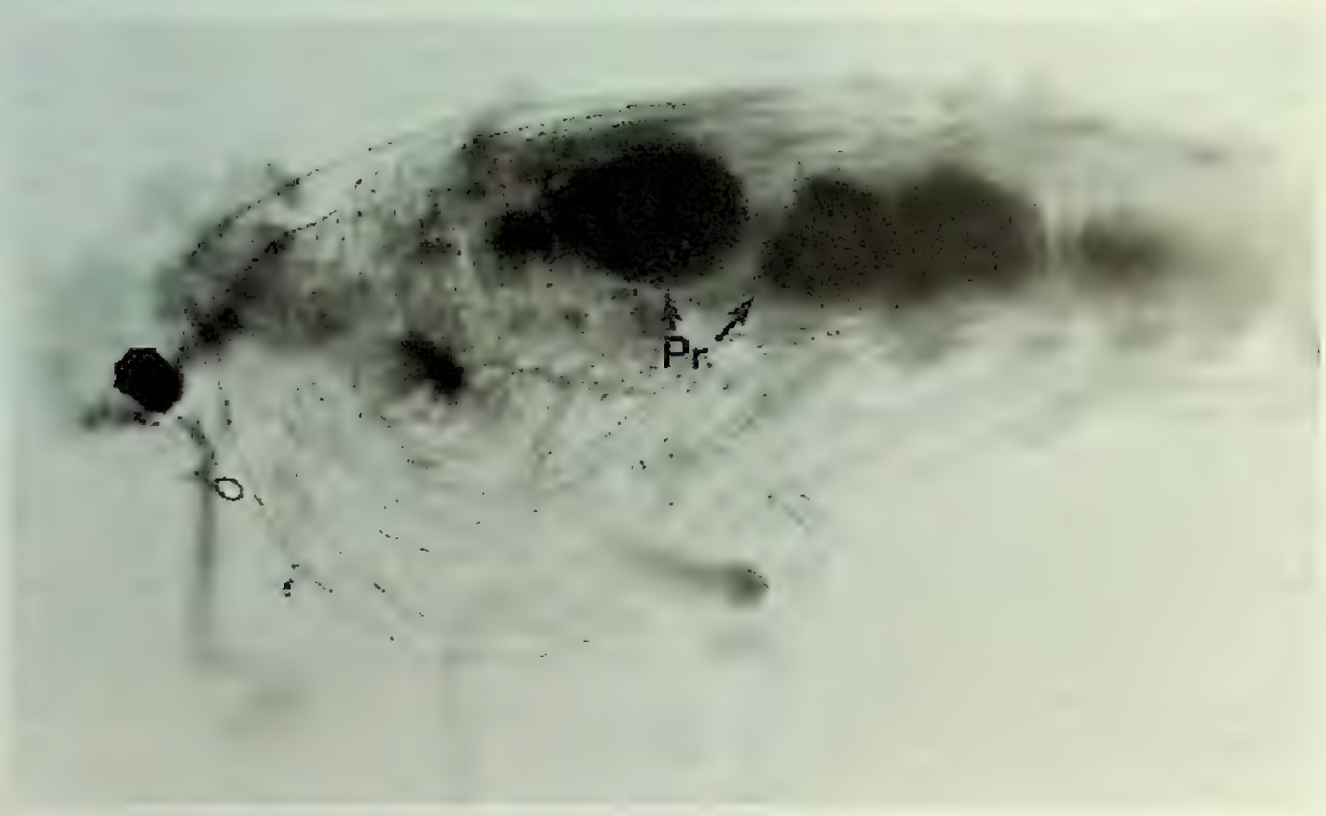

Figure 5. *Sinocalanus doerri* with procercoids (Pr) taken from the gut of a 17-mm striped bass. Photograph by the senior author.

that have never been exposed to this parasite (Sakanari and Moser 1990). Based on these results and the fact that cestodes typically evolve more slowly than their hosts, Sakanari and Moser proposed that adult striped bass from the Sacramento-San Joaquin Estuary were evolving resistance to *L. dollfusi* without corresponding adaptation by *L. dollfusi*. The encystment and lack of cellular response to *Proteocephalus* sp. plerocercoids by young striped bass in our study suggests a similar one-sided evolution of resistance in young striped bass to *Proteocephalus* sp. plerocercoids.

In Chesapeake Bay, where 79% of the YOY striped bass were infested with *S. pleuronectis*, mass mortalities were not seen, but loss of heavily infected fish could be a component of natural mortality (Paperna and Zwerner 1976). Similarly, striped bass mortalities have been associated with *L. dollfusi* parasitism and lesions formed by the shedding of rafts (Sakanari and Moser 1986, Sakanari and Moser 1990).

Despite the limited immune response of striped bass to plerocercoids, sublethal effects of parasitism may increase susceptibility to other stressors (Paperna and Zwerner 1976) and explain why mean intensity of plerocercoids in our fish increased with fish length until the relationship became asymptotic around 62 mm. Parasite loading may increase with age and size until mortality eliminates heavily infected fish. Alternatively, young striped bass may switch prey as they grow. However, the high prevalence of plerocercoids in striped bass in the fall indicates that some fish survive parasitism or may still be acquiring plerocercoids from their diet. We could not determine if plerocercoids affected abundance of young striped bass.

Interestingly, no plerocercoids occurred in 1,055 delta smelt, *Hypomesus transpacificus*, or 279 longfin smelt, *Spirinchus thaleichthys*, collected in the same

years as striped bass in our study. These smelt co-occur with striped bass and *S. doerri* and *E. affinis* are also major food items for them. Perhaps the relatively straight gut of the smelt does not retain procercoids long enough for further development to occur (Fig. 6).

Interannual variability of parasite prevalence rates could not be explained by environmental factors. The positive correlations between parasite prevalence and temperature suggest that temperature may influence the rate of infestation, possibly because striped bass feeding rates increase with temperature causing them to eat more copepods. Alternatively, temperature may influence the incidence of *Proteocephalus* sp. in the environment. However, because both striped bass length and temperature increase seasonally, this correlation may be spurious, merely reflecting the tendency for infestation to increase with fish size and age. Increased parasite prevalence at high Secchi disc readings may indicate that young striped bass can feed more efficiently on infected copepods when water transparency is high. In laboratory experiments, the ability of young striped bass to feed on copepods decreased as turbidity increased (Chesney 1989, Breitburg 1988). Interannual variation in prevalence was not associated with EC. Although river flows could affect the distribution of parasites, vectors, and fish, flow variables did not correlate well with interannual variations in plerocercoid prevalence.

Despite the likelihood that *S. doerri* and *E. affinis* are vectors, plerocercoid prevalence in striped bass did not correlate well with the concentrations of either species in the environment or diet. Possible explanations include: 1) The procercoid found in these copepods may not be the same species of cestode found in young bass. 2) Striped bass may obtain procercoids from a different zooplankton prey. 3) Prevalence of plerocercoids in striped bass reflects their feeding history which may not be adequately depicted by copepod abundance in the environment or their

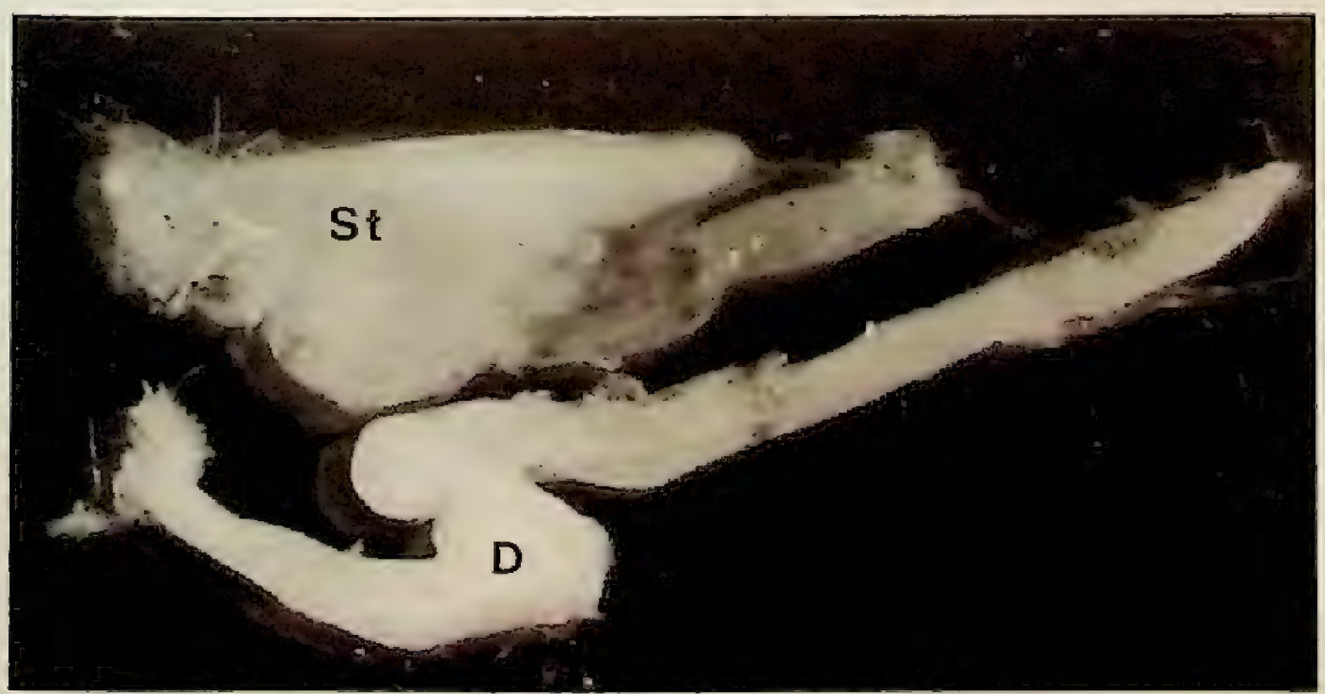

Figure 6. The relatively straight gut of a 27-mm delta smelt (D) versus the s-shaped gut of a 28-mm striped bass (St). Photograph by the senior author.

stomachs at the time of collection.

To better understand the effects of the plerocercoid tentatively identified as *Proteocephalus* sp., it needs to be identified to species and its life history and definitive host determined. Experiments should also be performed to determine effects of heavy infestations on young bass.

ACKNOWLEDGMENTS

M. Moser, University of California, Santa Cruz, originally identified the cestodes. C. Alexander, San Francisco State University, tentatively identified the plerocercoids. M. Nobriga patiently evaluated striped bass stomach contents and counted plerocercoids. D. Ostrach, University of California, Davis, prepared histological slides of infested striped bass. P. Law analyzed the data using S-PLUS. R. Fujimura and L. Miller initiated this study and L. Miller and D. Stevens commented on drafts. This work was supported by Federal Aid in Sport Fish Restoration Act funds, Grant F-51-R; the California Striped Bass Stamp Fund; the California Department of Water Resources; and the U.S. Bureau of Reclamation.

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Received: 20 December 1996
Accepted: 4 April 1997

California Fish and Game 83(3):118-127 1997

BACTERIAL SHELL DISEASE IN CRANGONID SHRIMP

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***Crangon franciscorum* and *C. nigricauda* collected from estuarine areas had shell lesions typical of bacterial shell disease. Most shrimp collected without lesions developed lesions in the laboratory, whereas some shrimp collected with lesions molted, leaving healthy exoskeleton. Histology and scanning electron microscopy revealed damage to the exoskeleton as well as to underlying tissues. New exoskeleton developed under lesioned exoskeleton, possibly preventing spread of lesions. *Crangon nigricauda* from Humboldt Bay had a higher prevalence (8%) of lesions than *C. franciscorum* (1.7 to 2.6%) from the Mad and Little River estuaries. Host immune responses included hemocyte infiltration, nodule formation, and melanization. Bacteria identified as *Vibrio* spp. and *Pseudomonas* sp. were associated with lesions.**

INTRODUCTION

Chitinoclastic bacteria are ubiquitous in the marine environment and are natural epibionts of crustaceans. These bacteria can produce a condition known as bacterial shell disease (Cook and Lofton 1973, Johnson 1983, Getchell 1989). Bacterial shell disease is probably the most common bacterial disease of crustaceans and cases have been documented in both wild and captive animals (Sindermann 1990). In previous studies, the prevalence and severity of bacterial shell disease lesions differed among species, sites, and years (Rosen 1970, Gopalan and Young 1975, Young and Pearce 1975, Brock and Lightner 1990, Sindermann 1990). One or more bacterial species of the genera *Vibrio*, *Pseudomonas*, and others are known to invade the crustacean cuticle, leading to lesions characteristic of bacterial shell disease (Johnson 1983, Sindermann 1990). The cuticle of affected crustaceans becomes brittle and eroded. Diseased shrimp exhibited rotting appendages and blackened areas of erosion on the exoskeleton. The brown to black color of affected areas results from deposition of melanin by hemocytes (Johnson 1983). If the uncalcified layer of the exoskeleton remains intact, molting effectively rids the crustacean of the disease (Johnson 1983). If not, the infection may involve soft tissue and result in mortality during molting.

Even though bacterial agents (low virulence, gram-negative, chitinoclastic bacteria) of shell disease are known, the etiology of the disease is complex. Shell disease is a result of interactions between facultative pathogens and environmental stress due to a degraded environment or to crowding (Sindermann 1990).

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Chitinoclastic bacteria need an entry point into the epicuticle as they do not normally affect unstressed, healthy individuals (Cook and Lofton 1973). The disease may result from (i) synergistic effects of lipolytic and chitinoclastic bacteria (Sindermann 1990), (ii) an entry site for chitinoclastic bacteria or fungi provided when the epicuticle is compromised by mechanical or chemical injury, or (iii) degradation of the epicuticle by pollutants which interfere with its proper formation or maintenance. In addition, pollutants may also interfere with the molting process (Brock and Lightner 1990).

We describe the difference in prevalence of bacterial shell disease in *Crangon franciscorum* from the Mad and Little River estuaries and *C. nigricauda* from Humboldt Bay in Humboldt County, California. We identify the causative agents and describe their effects on the shrimp. This is the first description of bacterial shell disease from crangonid shrimp from the Pacific Coast of the United States.

METHODS

Sampling gear varied with collection location. In Humboldt Bay, *C. nigricauda* were collected using a 5.0-m otter trawl with a 0.5-cm stretch mesh cod end. In the Mad and Little River estuaries, juvenile *C. franciscorum* were collected during low tides using dip nets or a beach seine. Shrimp were held in insulated, aerated coolers and transported live to the Telonicher Marine Laboratory, Trinidad, California. Counts of shrimp affected with bacterial shell disease were taken after collections to determine prevalences in wild shrimp.

Shrimp were held in round, static 284-liter tanks provided with sea water, aeration, and sponge filters. Chopped California mussel, *Mytilus californianus*, meats; whitebait smelt, *Allosmerus elongatus*; or brine shrimp, *Artemia salina*, were fed to shrimp every other day. Exuviae, mortalities, and excess food were periodically removed.

Material for bacterial isolation was collected with a sterile inoculating loop from lesions characteristic of bacterial shell disease on the exoskeleton of shrimp. The inoculum was streaked onto tryptic soy agar plates (TSA) containing 1.0% sodium chloride or marine agar (Difco) plates for primary isolation and was incubated at 23°C for 48 h. Biochemical tests (antibiotic and vibriostat [2,4-diamino 6,7-diisopropyo pteridine phosphate] sensitivity) were performed to identify pure cultures of isolated marine bacteria according to methods described by Baumann and Baumann (1981). The Analytical Profile Index (API)-20E system for identifying enteric bacteria was also used according to techniques described by Kent (1982). Prevalence of bacterial shell disease among sampled shrimp populations was compared with ANOVA and Fisher's multiple-comparison test using arcsine transformed data.

Shrimp without lesions and those with lesions characteristic of bacterial shell disease were sampled for histological and scanning electron microscopy (SEM) study. Shrimp used for histological study were preserved and dissected into segments according to procedures described by Bell and Lightner (1988). Specimens were fixed in Davidson's solution for 24-48 h, transferred to 70% ethyl alcohol (Bell and Lightner 1988), dehydrated through a series of tertiary butyl alcohols and then vacuum infiltrated with paraffin at 300 mm Hg. Deparaffinized 5-10-μm sections were stained using a regressive hematoxylin and eosin series (Humason 1979) or using Mallory's

stain for collagen (Luna 1968).

For SEM, shrimp were cut into pieces to reveal shell disease damage and fixed in buffered 2% glutataldehyde for 24-48 h, depending on the size of the specimen. After fixation, specimens were transferred to 70% ethyl alcohol, dehydrated in an ethyl alcohol series, and critical point dried. They were then embedded in paraffin and the exoskeleton was carved away with a scalpel to reveal underlying tissues (paraffin carving) (Oshel 1985).

RESULTS

Bacteria isolated from shell disease lesions were identified as *Vibrio* spp. (API-20 number = 0066600) and *Pseudomonas* sp. (API-20 number = 2062701) using the API system and other biochemical tests. D. Antonio (Department of Medicine and Epidemiology, School of Veterinary Medicine, University of California, Davis) verified bacterial identifications. *Vibrio* spp. were sensitive to the vibriostat chemical. Bacteria grew on TSA with 1.0% NaCl and marine agar, but did not grow on TSA without added salt, indicating salt was required for growth.

Mean prevalences of bacterial shell disease in *C. franciscorum* and *C. nigricauda* were significantly different ($F = 5.35$; $df = 2, 8$; $P < 0.05$) (Table 1). *Crangon nigricauda* from Humboldt Bay had significantly higher prevalences of shell disease ($\bar{x} = 8.0\%$, range = 4.4-29%) than *C. franciscorum* from the Mad and Little River estuaries ($\bar{x} = 1.7\%$ and 2.6%, range = 0.0-4.1% and 0.0-5.9%) (Fisher's multiple-comparison test, family error rate = 0.054). *Crangon franciscorum* were usually juveniles, whereas *C. nigricauda* were usually adults.

Shrimp without lesions when collected often developed lesions characteristic of shell disease within 24 h. The prevalence of shell disease in holding tanks was as high as 100% after 24 h. Many shrimp also molted within 24 h of being collected. Whether or not this was a result of stress from capture and handling or normal molting

Table 1. Prevalence of bacterial shell disease in *Crangon franciscorum* from the Mad and Little River estuaries, California and in *C. nigricauda* from Humboldt Bay, California from May 1989 to September 1991. NS indicates that no shrimp were sampled for bacterial shell disease. Numbers in parentheses are number infected/total number collected.

	Crangon franciscorum		*Crangon nigricauda*
Date	Mad River	Little River	Humboldt Bay
5/89	NS	NS	4.4% (29/654)
1/90	NS	0% (0/35)	NS
6/90	NS	0% (0/212)	NS
8/90	NS	0.5% (1/207)	NS
10/90	NS	5.9% (23/392)	NS
4/91	NS	NS	9.9% (21/213)
7/91	0% (0/120)	NS	29.0% (27/92)
8/91	0% (0/170)	NS	NS
9/91	4.1% (8/193)	1.2% (2/163)	NS
Total	1.7% (8/483)	2.6% (26/1009)	8.0% (77/959)

was not determined. While in captivity, some infected shrimp shed or reduced the size of lesions during ecdysis. Exuviae with lesions were found in tanks from shrimp that no longer had any lesions.

Shrimp affected with bacterial shell disease were readily distinguished from healthy shrimp. Normal exoskeletons contained chromatophores with dispersed pigment that were dark and stellate and chromatophores with aggregated pigment that had white stellate areas with dark centers (Fig. 1). Exoskeleton adjacent to disease areas was darkened; melanized; and often rounded, cracked, eroded, or somewhat amorphous (Figs. 2-4). Affected areas were brown to black and, in some cases of severe lesions, the surrounding soft tissue was white or pink.

Tissue damage from bacterial shell disease varied with the area infected and severity of the lesion. Infections on appendages were typically small, but microscopic examination often revealed severe damage to underlying tissue (Fig. 2). Infections involving larger areas frequently had melanization near the lesion (Fig. 3). Depending on the severity of the lesion, cracking around the affected area (Fig. 4) was sometimes present, as was involvement of underlying tissue. One lesion had an unidentified fungus infection and a vorticellid was observed associated with a severe lesion. These were considered secondary invaders of large, badly deteriorated lesions.

Effects of lesions on shrimp were evident in histological sections. In unaffected exoskeleton, chromatophores appeared as discrete stellate packages of black pigment (Fig. 5). Normal exoskeleton was composed of several layers with no blackened areas except for chromatophores. Involvement of soft tissue was observed in many lesions. Lesions that involved only exoskeleton, with new exoskeleton forming underneath, also were observed. In minor lesions, loss of a portion of the exoskeleton was usually evident, but little damage was observed in underlying layers (Fig. 6). Many minor infections on appendages and antennae were composed of necrotic soft tissue and resulted in the loss of the distal portion of the appendage. Moderately severe lesions usually involved more of the exoskeleton and involvement of soft tissue was often evident (Fig. 7). In very severe lesions, the exoskeleton, epidermis, and underlying tissue were visibly destroyed (Fig. 8).

Melanin and hemocytes appeared in histological sections in response to infection. Small circular "foci" of melanin, not associated with chromatophores, were observed in histological sections near bacterial shell lesions (Fig. 6). Some severe wounds were characterized by hemocytes surrounding possible bacterial colonies (Fig. 9).

Some effects of bacterial shell disease could be seen with SEM. Although necrosis of underlying tissue was not evident with SEM, this method clearly illustrated pits and cracks of the exoskeletal surface that contained bacteria (Fig. 10). In paraffin-carved specimens, degradation of the exoskeleton and necrotic underlying tissues were revealed. Ultrastructure of tissues could be readily distinguished in paraffin-carved specimens (Fig. 11-14). Relatively undamaged exoskeleton (Fig. 11 and 12) could be differentiated from affected areas (Fig. 13 and 14). Layers of the exoskeleton were distinct in unaffected areas, especially when compared to adjacent affected areas (Fig. 12 and 14). Degradation of the exoskeleton by bacteria was evidenced by the lack of layering (Fig. 14).

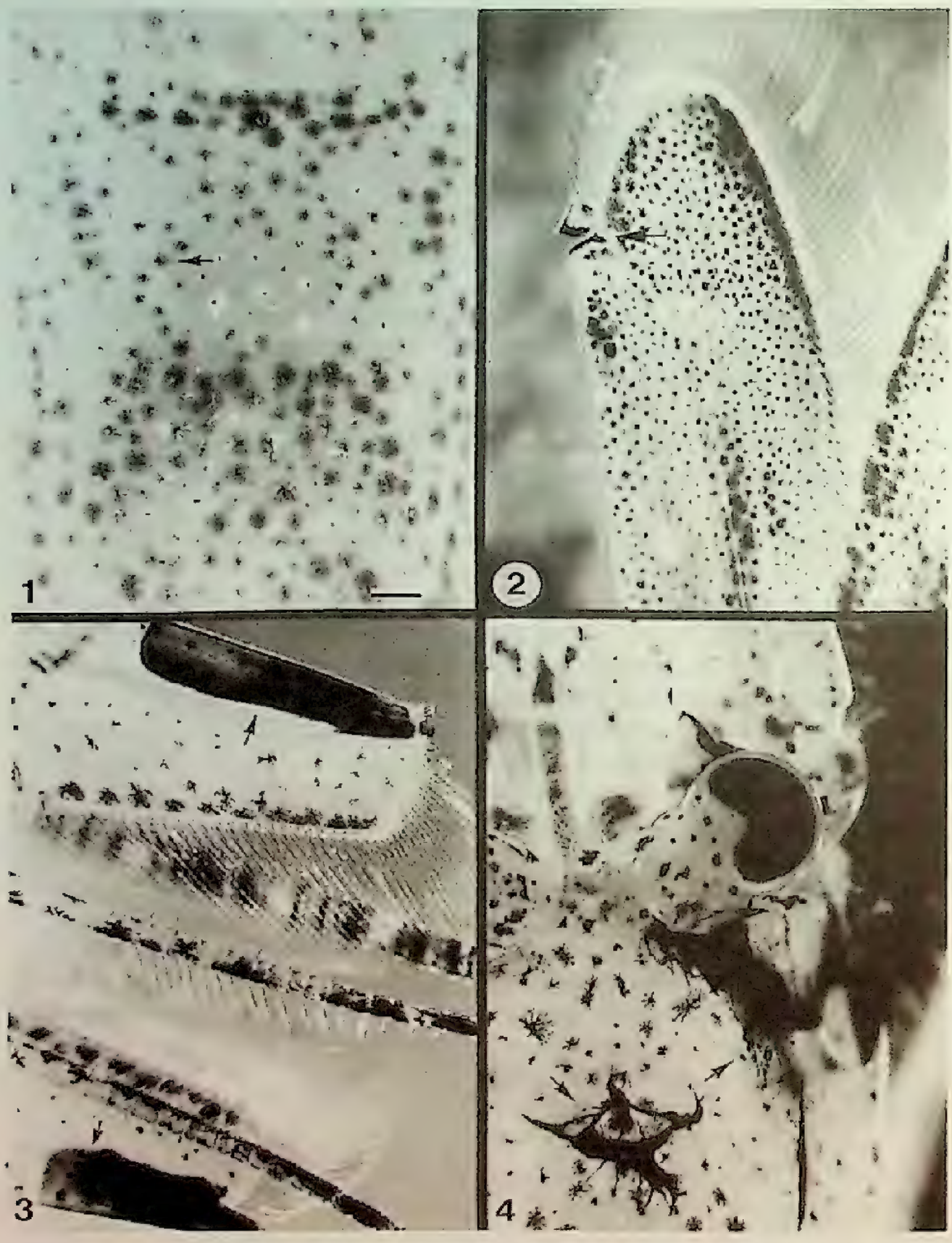

Figure 1. Normal exoskeletal exterior of *C. franciscorum* showing stellate configuration of chromatophores (arrow). Bar = 0.5 mm (scale is the same for Fig. 2-4).
Figure 2. Minor bacterial shell disease lesion on the uropod of *C. franciscorum* (arrow).
Figure 3. Moderate bacterial shell disease lesion on antennules of *C. franciscorum* (arrows).
Figure 4. Severe bacterial shell disease lesion on carapace of *C. franciscorum.* Note melanin not released from chromatophores (arrows). All photographs by the senior author.

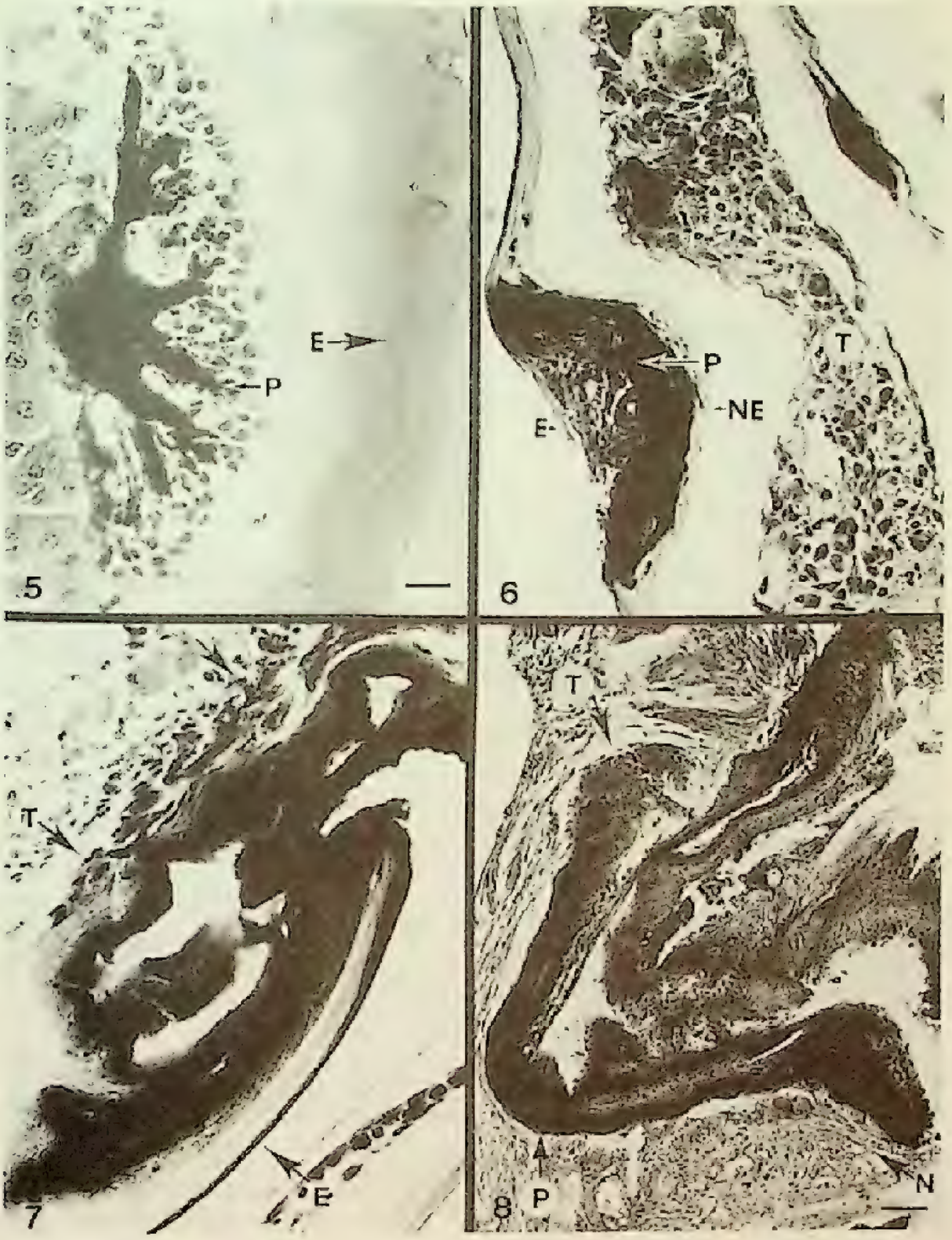

Figure 5. Cross section of normal exoskeleton (E) from the carapace of *C. nigricauda*. Exoskeleton is undamaged and melanin is found inside the chromatophore (P). Bar = 20 µm (scale is the same for Fig. 6 and 7).

Figure 6. Small bacterial shell disease lesion on the uropod of *C. nigricauda*. The exoskeleton (E) has been eroded away above the wound and melanin (P) is in the wound. The underlying soft tissue (T) is slightly damaged. A layer of new exoskeleton (NE) is forming underneath the lesion.

Figure 7. Moderate bacterial shell disease lesion on second abdominal segment of *C. nigricauda* showing loss of underlying soft tissue (T). The lesion is spreading across the surface of the exoskeleton (E), as can be noted by the black layer.

Figure 8. Severe bacterial shell disease lesion on fourth abdominal segment of *C. nigricauda*. Note the loss of tissue (T), melanization (P) of the wound, and muscle necrosis (N). Bar = 50 µm. All photographs by the senior author.

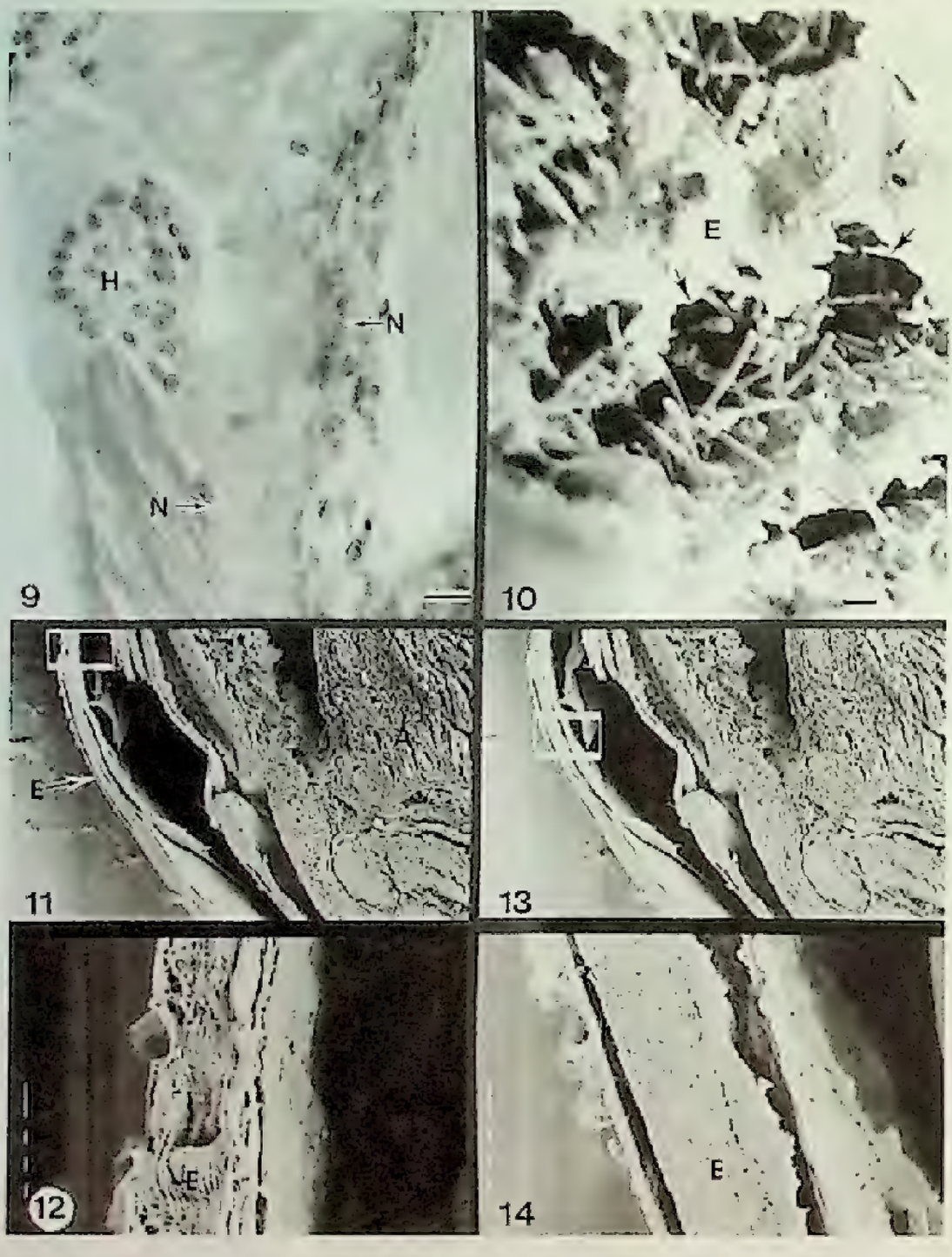

Figure 9. Hemocytes (H), stained with hematoxylin and eosin, surrounding an apparent core of bacteria or cell debris from a lesion. Muscle necrosis (arrows) is evident. Bar = 10 µm.
Figure 10. Scanning electron micrograph of the surface of a lesion on the exoskeleton (E) from *C. franciscorum*. Note pits containing bacteria (arrows). Bar = 1.0 µm.
Figure 11. Scanning electron micrograph of unaffected exoskeletal layers (E) from the second abdominal segment of *C. nigricauda*. Abdominal musculature (A) is readily distinguished from exoskeleton. Box frames the close-up area of normal exoskeleton shown in Figure 12.
Figure 12. Scanning electron micrograph of unaffected area of the exoskeleton from the second abdominal segment of *C. nigricauda*. Layers of the exoskeleton (E) are readily distinguished. Bar = 100 µm.
Figure 13. Scanning electron micrograph of exoskeletal layers (E) from a lesion on the second abdominal segment of *C. nigricauda*. Box frames the close-up area of affected exoskeleton shown in Figure 14.
Figure 14. Scanning electron micrograph of exoskeleton (E) degraded by a lesion from thesecond abdominal segment of *C. nigricauda*. Note the loss of layering in the exoskeleton. Bar =100 µm.
All photographs by the senior author.

DISCUSSION

The appearance of affected tissues varies with the severity of bacterial shell disease. Histological examination revealed cracking and pitting of the exoskeleton. Once the uncalcified (endocuticle) layer was penetrated, agglutinated blood cells filled the proximal portion of the lesion. If the exoskeleton and epidermis were destroyed, inner tissues were also necrotic. Unidentified fungi were secondary invaders of advanced lesions. We identified *Vibrio* spp. and *Pseudomonas* sp. from areas in and around lesions, but not from healthy exoskeleton.

The extent of damage to underlying tissue and the host immune response varied with lesion severity and location. In minor lesions, damage was mainly limited to the exoskeleton with little effect on underlying tissues. Larger lesions typically exhibited the most soft tissue damage. Lesions on appendages were generally small, but loss of the distal portion of the appendage was common. In histological sections of appendages, damage appeared extensive with both the exoskeleton and underlying tissue often involved. If the infection was limited to the epicuticle, shrimp could effectively shed the infection by molting, but more severe damage could cause mortality.

Shrimp commonly developed lesions while being held in tanks in the laboratory. Bacteria probably invaded wounds received during collecting, handling, transporting, and rearing. Infections may have been the result of damage or abrasions from crowding whereby the protective epicuticle was punctured, providing an entry point for chitinoclastic bacteria (Cook and Lofton 1973). Lipolytic bacteria may have eroded away the epicuticle, leaving the procuticle vulnerable to chitinoclastic bacteria (Sindermann 1990). New infections in recently molted shrimp could be a result of wounds to the soft exoskeleton.

We found that the prevalence of shell disease lesions varied in wild populations of *C. franciscorum* from the Mad and Little River estuaries and *C. nigricauda* from Humboldt Bay. This could result from differences in life histories (Breed and Olsen 1977, Jay 1989) or differences in environmental variables such as salinity and pollutants. In our study, *C. franciscorum* were typically juveniles while *C. nigricauda* were typically adults, which molt less frequently. Bacterial shell disease may be more prevalent in adult shrimp than in juveniles which molt frequently and can shed lesions readily (Brock and Lightner 1990). Thus, the higher prevalence of shell disease observed in Humboldt Bay may be attributed to the reduced molting frequency of the adult *C. nigricauda* that we collected there.

The higher salinity of Humboldt Bay (<25 - >34 ppt) (Barnhart et al.[2] 1992) compared to the Mad and Little River estuaries (8-19.5 ppt) may have affected the prevalence of bacterial shell disease lesions in the two areas. Because bacteria responsible for shell disease required salt to grow in laboratory cultures, the higher prevalence of lesions found in *C. nigricauda* may be a result of the higher salinity in Humboldt Bay where we collected this species, which cannot tolerate salinities below

[2] Barnhart, R. A., M.J. Boyd, and J.E. Pequegnat. 1992. Ecology of Humboldt Bay, California: An estuarine profile. USFWS Biological Report 1.

19 ppt (Simenstad 1983). Conversely, *C. franciscorum* is a euryhaline species utilizing the upper portions of estuaries, such as the Mad and Little River estuaries, as nursery areas. This preference for low-salinity areas may reduce the vulnerability of *C. franciscorum* to bacterial shell disease.

Pollution has been cited as a contributor to high bacterial counts and bacterial shell disease (Gopalan and Young 1975, Young and Pearce 1975, Sindermann 1990) and may be a factor in the variation of lesion prevalence that we observed between *C. nigricauda* and *C. franciscorum*. The manner in which pollution facilitates the development of bacterial shell disease is not exactly known. However, mechanical damage to the cuticle, growth enhancement of chitinoclastic bacteria, and lodging of bacteria in pores or ducts have all been postulated as promoters of the disease (Gopalan and Young 1975, Sindermann 1990).

Sources of pollution in Humboldt Bay where we collected *C. nigricauda* include (i) the City of Eureka wastewater discharge into South Humboldt Bay, (ii) commercial and sport fishing boats that use Humboldt Bay and its marina, and (iii) runoff from agricultural operations surrounding Humboldt Bay. In contrast, Mad and Little rivers, where we collected *C. franciscorum*, have fewer agricultural operations and limited boat traffic.

We conclude that differences in the prevalence of bacterial shell disease probably does not result from a difference in susceptibility between species, but rather from environmental differences. Bacteria associated with the disease are marine species and typically invade wounds and not healthy exoskeleton. Therefore, the co-occurrence of a shrimp species with a high salinity preference and the substantial pollution in Humboldt Bay most likely led to the higher incidence of bacterial shell disease there. To fully understand the differences in prevalence of bacterial shell disease, the range of salinity in which infected shrimp are found, as well as the occurrence of chitinoclastic bacteria and associated pollution, need to be determined.

ACKNOWLEDGMENTS

The Telonicher Marine Laboratory of Humboldt State University partially supported this research. We thank T. Newhouse, M. Bourandas, N. Sligh, L. Rusconi, and D. Hoskins for their help in collecting and maintaining shrimp. D. Antonio identified the bacteria.

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Received: 2 October 1996
Accepted: 10 October 1997

California Fish and Game 83(3):128-129 1997

CONVERSIONS BETWEEN TOTAL, FORK, AND STANDARD LENGTHS FOR LINGCOD, *OPHIODON ELONGATUS*

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Although lingcod, *Ophiodon elongatus*, is an important commercial and recreational species (Silberberg and Adams 1993), there is a lack of consistency in the units used to record length. Total length, fork length, and standard length have all been used, but data were produced that are not easily comparable. Here, we present relationships between total length, fork length, and standard length for lingcod.

All measurements were from specimens collected off central California. Adult and subadult lingcod were collected from the recreational lingcod fishery from Pt. Año Nuevo to Pt. Reyes. Pelagic juveniles were collected from midwater trawls conducted from Pt. Sur to Pt. Reyes. Benthic juveniles were collected in San Francisco Bay using beach seines and bottom trawls. Total length was measured from the anterior tip of the lower jaw to the posterior tip of the longest rays of the caudal fin. Fork length was measured from the anterior tip of the lower jaw to the posterior end of the shortest caudal ray. Standard length was measured from the anterior tip of the lower jaw to the posterior end of the hypural bone.

Linear regressions of the form y = slope(x) + (y-intercept) were estimated using non-linear least squares (Systat 1996) for all combinations of measurements (Table 1, Fig. 1). All regressions were highly significant ($r^2 > 0.999$). We found no significant difference in the regression slopes between males and females (ANOVA for homogeneity of slopes). To use the data, place the corresponding variables into the above formula. For example, to determine the standard length of a 684-mm total length lingcod, use the following equation:

Standard length = 0.873(684 mm) + 0.3 mm = 597.4 mm.

Table 1. Length parameters for linear regressions computed between total length, fork length, and standard length for lingcod.

	Slope	y-intercept (mm)	Sample size	Size range (mm)	MSE
Fork length from total length	0.981	-0.521	619	23-1046	8.029×10^{7}
Total length from fork length	1.019	0.562	619	23-1046	8.301×10^{7}
Standard length from total length	0.873	0.308	578	23-933	4.986×10^{7}
Total length from standard length	1.145	-0.286	578	23-933	6.532×10^{7}
Standard length from fork length	0.889	0.884	555	23-933	4.989×10^{7}
Fork length from standard length	1.124	-0.942	555	23-933	6.275×10^{7}

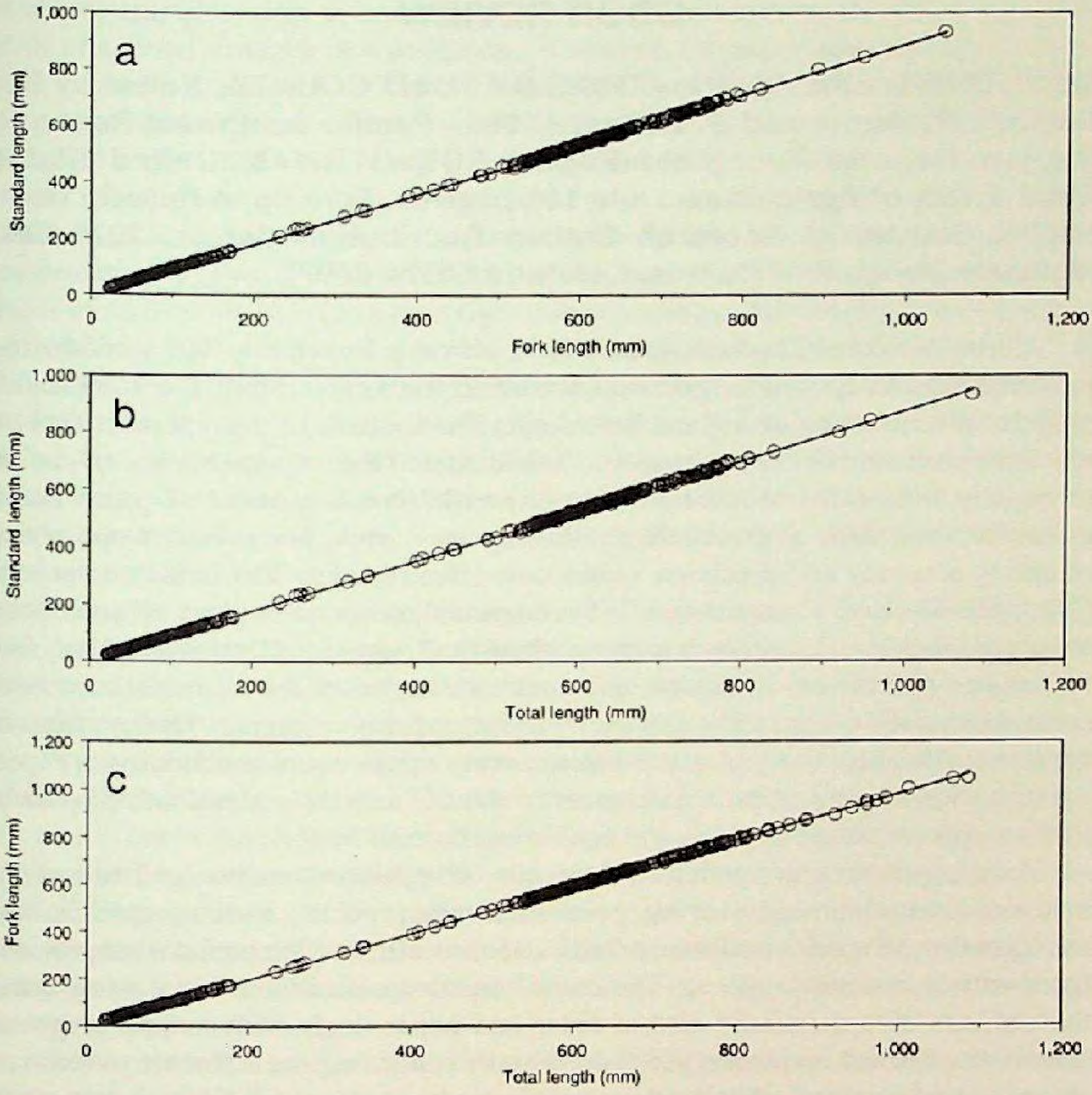

Figure 1. Plots of (a) standard length and fork length, (b) standard length and total length, (c) and fork length and total length for lingcod. Open circles represent measured values. Solid lines indicate predicted values from the two linear regressions created between the independent and dependent variables (from Table 1). The two lines are so similar that they appear as one.

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Received: 27 March 1997
Accepted: 12 July 1997

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